

CANADIAN THESES ON MICROFICHE

THÈSES CANADIENNES SUR MICROFICHE



National Library of Canada
Collections Development Branch

Canadian Theses on
Microfiche Service

Ottawa, Canada
K1A 0N4

Bibliothèque nationale du Canada
Direction du développement des collections

Service des thèses canadiennes
sur microfiche

NOTICE

The quality of this microfiche is heavily dependent upon the quality of the original thesis submitted for microfilming. Every effort has been made to ensure the highest quality of reproduction possible.

If pages are missing, contact the university which granted the degree.

Some pages may have indistinct print especially if the original pages were typed with a poor typewriter ribbon or if the university sent us an inferior photocopy.

Previously copyrighted materials (journal articles, published tests, etc.) are not filmed.

Reproduction in full or in part of this film is governed by the Canadian Copyright Act, R.S.C. 1970, c. C-30. Please read the authorization forms which accompany this thesis.

**THIS DISSERTATION
HAS BEEN MICROFILMED
EXACTLY AS RECEIVED**

AVIS

La qualité de cette microfiche dépend grandement de la qualité de la thèse soumise au microfilmage. Nous avons tout fait pour assurer une qualité supérieure de reproduction.

S'il manque des pages, veuillez communiquer avec l'université qui a conféré le grade.

La qualité d'impression de certaines pages peut laisser à désirer, surtout si les pages originales ont été dactylographiées à l'aide d'un ruban usé ou si l'université nous a fait parvenir une photocopie de qualité inférieure.

Les documents qui font déjà l'objet d'un droit d'auteur (articles de revue, examens publiés, etc.) ne sont pas microfilmés.

La reproduction, même partielle, de ce microfilm est soumise à la Loi canadienne sur le droit d'auteur, SRC 1970, c. C-30. Veuillez prendre connaissance des formules d'autorisation qui accompagnent cette thèse.

**LA THÈSE A ÉTÉ
MICROFILMÉE TELLE QUE
NOUS L'AVONS REÇUE**



National Library
of Canada

Bibliothèque nationale
du Canada

Ottawa, Canada
K1A 0N4

TC -

ISBN 0-315-01005-X

CANADIAN THESES ON MICROFICHE SERVICE - SERVICE DES THÈSES CANADIENNES SUR MICROFICHE

PERMISSION TO MICROFILM - AUTORISATION DE MICROFILMER

• Please print or type - Écrire en lettres moulées ou dactylographier

AUTHOR - AUTEUR

Full Name of Author - Nom complet de l'auteur

DALE LAUER STELTER

Date of Birth - Date de naissance

MAY 7, 1955

Canadian Citizen - Citoyen canadien

☒ Yes / Oui

☐ No / Non

Country of Birth - Lieu de naissance

CANADA

Permanent Address - Résidence fixe

Box 18, Site 2, R.R. 1
Omanan, Alberta
T0C 1V0

THESIS - THÈSE

Title of Thesis - Titre de la thèse

APPLICATION OF THE SABOWA GROWTH SIMULATOR TO UPLAND WHITE SPRUCE-TREMBLING ASPENS
STANDS IN ALBERTA

Degree for which thesis was presented
Grade pour lequel cette thèse fut présentée

MASTER OF SCIENCE

Year this degree conferred
Année d'obtention de ce grade

1985

University - Université

UNIVERSITY OF ALBERTA

Name of Supervisor - Nom du directeur de thèse

KENNETH O. HIGGINBOTOM / BARRIE L. PHILLIPS

AUTHORIZATION - AUTORISATION

Permission is hereby granted to the NATIONAL LIBRARY OF CANADA to
microfilm this thesis and to lend or sell copies of the film.

The author reserves other publication rights, and neither the thesis nor exten-
sive extracts from it may be printed or otherwise reproduced without the
author's written permission.

L'autorisation est, par la présente, accordée à la BIBLIOTHÈQUE NATIONALE
DU CANADA de microfilmer cette thèse et de prêter ou de vendre des ex-
emplaires du film.

L'auteur se réserve les autres droits de publication; ni la thèse ni de longs ex-
traits de celle-ci ne doivent être imprimés ou autrement reproduits sans
l'autorisation écrite de l'auteur.

ATTACH FORM TO THESIS - VEUILLEZ JOINDRE CE FORMULAIRE À LA THÈSE

Signature

Dale Lauer

Date

APRIL 13, 1985

THE UNIVERSITY OF ALBERTA

Application of the JABOWA growth simulator to upland white
spruce-trembling aspen stands in Alberta

by



Dale Elder Stelter

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
OF MASTER OF SCIENCE

Department of Forest Science

EDMONTON, ALBERTA

Spring 1985

THE UNIVERSITY OF ALBERTA

RELEASE FORM

NAME OF AUTHOR Dale Elder Stelter
TITLE OF THESIS Application of the JABOWA growth
simulator to upland white spruce-
trembling aspen stands in Alberta
DEGREE FOR WHICH THESIS WAS PRESENTED MASTER OF SCIENCE
YEAR THIS DEGREE GRANTED Spring 1985

Permission is hereby granted to THE UNIVERSITY OF
ALBERTA LIBRARY to reproduce single copies of this
thesis and to lend or sell such copies for private,
scholarly or scientific research purposes only.

The author reserves other publication rights, and
neither the thesis nor extensive extracts from it may
be printed or otherwise reproduced without the author's
written permission.

(SIGNED) *Dale Elder Stelter*.....

PERMANENT ADDRESS:

Box 18, Site 2, R.R. 1.....

Onoway, ALBERTA.....

T0E 1V0.....

DATED ... *April 18* 1985

THE UNIVERSITY OF ALBERTA
FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled Application of the JABOWA growth simulator to upland white spruce-trembling aspen stands in Alberta submitted by Dale Elder Stelter in partial fulfilment of the requirements for the degree of MASTER OF SCIENCE.

Kenneth C. Higgins

Co-supervisor

Bernie L. Phillips

Co-supervisor

G. H. G. O. R.

Date... *April 18, 1988*

DEDICATION

This thesis is dedicated to the memory of my late grandmother, Mary Eva Hall, who as always, took the time to listen, share, and understand. It is also dedicated to my family, for their endless encouragement and understanding.

Abstract

Version II of the JABOWA forest growth model (Botkin et al. 1971, 1972a,b) has been modified to successfully reproduce species frequencies, diameter distributions, and basal areas during succession for upland white spruce (*Picea glauca* (Moench) Voss)-trembling aspen (*Populus tremuloides* Michx.) stands in Alberta. The resulting model, called JABOR, is mainly conceptual in nature, is stochastic, and falls within the distance-independent individual tree classification of Munro (1974). Annual diameter increment of tree growth is based upon species, tree size, allocation of available light among trees on the plot, competition for space and nutrients, and climatic effects.

Relatively little modification to the assumptions and mathematical relationships of JABOWA was required. The main difficulties encountered were in obtaining reliable and accurate program data. Also, no verification data were available for very young or very old stands. Above-ground living biomass predictions of the JABOR model support the Shifting-Mosaic Steady State model of living biomass accumulation of Bormann and Likens (1979a,b).

The model closely duplicated the results of a selected field study (Steneker 1974), and was used to point out unusual growth conditions in another (Lees 1966). It was also applied to a hypothetical research question dealing with response of white spruce to various trembling aspen removal treatments.

An examination of the model results, in conjunction with an analysis of the assumptions and mathematical relationships used, led to questioning of conventional or "classical" theory regarding the ecological processes and mechanisms that result in species sequences during succession. Support for most aspects of recent or contemporary theory was indicated.

ACKNOWLEDGEMENTS

I am very grateful to the following people and organizations:

1. My supervisors, Dr. Kenneth Higginbotham and Professor Barrie Phillips, for the many hours of their time, and their assistance and patience in seeing this thesis through to its completion.
2. Dr. George La Roi, of the Department of Botany, for serving as a member of my committee.
3. The Department of Forest Science, University of Alberta, and the Canadian Forestry Service, for funding this project through the Canadian Forestry Service Block Grant.
4. The Alberta Forest Service, and Proctor and Gamble Cellulose, Ltd., of Grande Prairie, Alberta, for the use of their permanent sample plot data.
5. Mr. Robert Morton, for the use of his temporary sample plot data, and for making available the Alberta Forest Service and Proctor and Gamble Cellulose, Ltd., permanent sample plot data.

Chapter	Table of Contents	Page
I.	INTRODUCTION	1
A.	PURPOSE AND OBJECTIVES	5
	Purpose of Project	5
	Limitations	6
	Justification	6
	Justification for Choosing JABOWA	7
	Objectives	8
II.	LITERATURE REVIEWS	9
A.	ACCUMULATION OF LIVING BIOMASS IN FOREST ECOSYSTEMS	9
	Asymptotic Model	9
	Shifting-Mosaic Model	10
B.	SPECIES SEQUENCES DURING SUCCESSION	16
	Historical Review and Development of Classical Theory	17
	Contemporary Theory	19
III.	DESCRIPTION OF JABOWA	26
A.	BASIC MODEL STRUCTURE AND PARAMETERS	26
B.	GENERAL DESCRIPTION OF PROGRAM AND FUNCTIONAL RELATIONSHIPS	28
C.	RESULTS AND VALIDATION	36
D.	LIMITATIONS AND WEAKNESSES	36
IV.	METHODS	39
A.	BASIS OF THE JABOR MODEL	39
B.	SPECIES USED	39
C.	OVERVIEW OF METHODOLOGY	41
D.	DATA COLLECTION AND PROGRAM CHANGES	42

Environmental Parameters and Functions	42
Tree Species Parameters and Functions	45
E. Collection of Validation Data	61
F. VALIDATION PROCEDURES AND OBTAINING OF RESULTS	65
V. RESULTS AND DISCUSSION	68
A. TREMBLING ASPEN	68
Basal Area	68
Frequency	74
Diameter Distribution	78
Biomass	83
B. WHITE SPRUCE	85
Basal Area	85
Frequency	88
Diameter Distribution	92
Biomass	96
C. TOTAL PLOT	96
Basal Area	96
Frequency	99
Biomass	102
D. GENERAL ASSESSMENT OF THE MODEL	109
E. POSSIBILITIES FOR EXTENSION OF THE MODEL	115
VI. FOREST MANAGEMENT APPLICATIONS OF THE MODEL	118
A. CASE STUDY I: Steneker (1974)	119
B. CASE STUDY II: Lees (1966)	126
C. CASE STUDY III: Investigation of Hypothetical Topic	132

VII. APPLICATION TO THEORY REGARDING MECHANISMS AND PROCESSES PRODUCING SPECIES SEQUENCES DURING SUCCESSION	141
VIII. SUMMARY AND CONCLUSIONS	149
Literature Cited	152
IX. APPENDIX I: FLOW CHART FOR JABOWA (VERSION II) AND GENERAL SUMMARY OF PROGRAM BY SUBROUTINE	160
X. APPENDIX II: SOURCE LISTING FOR JABOR, SAMPLE RUN, AND INDEX OF PARAMETERS THAT CAN BE CHANGED INTERACTIVELY	163
XI. APPENDIX III: LIVING BIOMASS EQUATIONS USED IN JABOR	178
XII. APPENDIX IV: TABLES OF RESULTS	180
XIII. APPENDIX 5: CASE STUDY DATA	184

List of Tables

<u>Table</u>	<u>Page</u>
1. Data collected for environmental parameters used in JABOR.....	43
2. Data collected for tree species parameters used in JABOR.....	46
3. Diameter limits and probability levels used in the size-dependent mortality function of JABOR.....	54
4. Distribution of validation plots by age class	64
5. Comparison of JABOR predictions of average diameter distribution per age class of trembling aspen to average diameter distribution of the validation data.....	79
6. Examples of stochastic variation in the predictions of JABOR for basal area of white spruce.....	87
7. Comparison of JABOR predictions of average diameter distribution per age class of white spruce to average diameter distribution of the validation data.....	93
8. Case Study I: comparison of JABOR predictions of response of average basal area of white spruce on control and treatment plots to field study results (Steneker 1974)...	123
9. Case Study II: average annual diameter increment of control and treated white spruce trees in field study (Lees 1966).....	129
10. Case Study II: predicted average annual diameter increment of control and treated white spruce trees	129
11. Case Study III: predicted average basal area of white spruce per age of removal of trembling aspen; plus year of maximum average basal area of white spruce per age of removal, and year of maximum mean annual increment of basal area of white spruce per age of removal.....	134

12. Case Study III: recovery of average basal area of trembling aspen after complete removal, by age of treatment.....	140
--	-----

List of Figures

<u>Figure</u>	<u>Page</u>
1. Living biomass accumulation with time, Asymptotic Curve Model.....	11
2. Living biomass accumulation with time, Shifting-Mosaic Steady State Model (from Bormann and Likens 1979a).....	14
3. Time-dependent solution of the diameter growth rate equation used in JABOWA (Version II).....	34
4. Comparison of JABOR predictions of average basal area by age class for trembling aspen to average basal area values of the validation data.....	69
5. Predictions of average basal area by age class for trembling aspen between 30 and 500 years.....	73
6. Comparison of JABOR predictions of average frequency by age class for trembling aspen to average frequencies of the validation data.....	75
7. Predictions of average frequency by age class for trembling aspen between 30 and 500 years.....	76
8. Predictions of average biomass by age class for trembling aspen between 30 and 500 years.....	84
9. Comparison of JABOR predictions of average basal area by age class for white spruce to average basal area values of the validation data.....	86
10. Predictions of average basal area by age class for white spruce between 30 and 500 years.....	89
11. Comparison of JABOR predictions of average frequency by age class for white spruce to average frequencies of the validation data.....	90
12. Predictions of average frequency by age class for white spruce between 30 and 500 years.....	91

13. Predictions of average biomass by age class for white spruce between 30 and 500 years	97
14. Comparison of JABOR predictions of average total plot basal area by age class to average basal area values of the validation data, plus JABOR predictions between 210 and 500 years.....	98
15. Comparison of JABOR predictions of average total plot frequency by age class to average frequencies of the validation data, plus JABOR predictions between 210 and 500 years.....	100
16. Predictions of average total plot biomass by age class between 30 and 500 years.....	103

I. INTRODUCTION

As the emphasis of forest land management in North America moves from a primarily timber-oriented basis to one of multiple land use, the importance of ecological knowledge and considerations has increased. Ecological principles governing forest establishment, succession, and growth are basic to managing forests for whatever purpose and scale, and apply particularly to areas concerning silvicultural practices (Spurr and Barnes 1980).

Interest in ecosystem succession has increased in recent years, especially regarding secondary succession (Corns and La Roi 1976). Researchers are finding that studies of succession have numerous theoretical applications to topics such as ecosystem diversity, stability, structure, and productivity (Spurr and Barnes 1980). Forest managers are discovering that knowledge of succession in the forests they tend can allow them to manipulate these stands toward desired ends, with improved returns on cost, labor, and yield.

Another recent trend in the field of forestry has been an increase in the use of computers in the development and utilization of forest growth models. This trend began in the 1960's, with the appearance of computers that could perform elaborate calculations and handle large amounts of data (Shugart and West 1980; Shugart et al. 1980). As computing power and availability have increased, and the cost of computing time has decreased, more models have been

developed, and computer modelling has become an integral tool in forest management on a world-wide scale (Munro 1974). The most important uses of forest growth models are in predicting the growth and yield of forest stands, and in analysing alternative management practices and hypotheses. Forest growth models are thus an effective pre-planning tool, and offer great potential for improved and informed forest resource management. A result of the development of forest growth models and increased interest in the investigation of ecosystem dynamics has been the development of forest succession models. Such models aid in deriving insights into the nature of long-term ecosystem dynamics, and enable consideration of the responses of a forest to alternative ecological situations.

Forest growth models can be classified by the unit of the forest for which growth is estimated. Munro (1974) proposed two categories: individual tree growth models, which are sub-divided into distance dependent and distance independent models, and stand growth models.

Individual tree growth models use the individual tree as the basic unit of growth, and stand growth is obtained by summing the growth of all individuals. Distance dependent models depend on individual tree location data for assessment of competition and calculation of tree growth, and often produce detailed information on tree crown and bole form, and stand structure (Munro 1974; Shugart and West 1980). They are generally designed for commercial forestry

operations, and thus may be less applicable to ecological studies (Shugart et al. 1980). The major disadvantage of such models is that the level of detail required on individual tree location makes data collection expensive and time-consuming, and requires excessive computer time. Examples of distance dependent growth models are those of Ek and Monserud (1974a,b), Hegyi (1974), and Mitchell (1975).

Distance independent growth models do not require data on tree location, and therefore are not particularly complex. These models tend to emphasize ecological processes and phenomena, and are often useful for studies of forest succession (Shugart and West 1980). The major advantage of distance independent models is their relative simplicity, which reduces computing time and permits rapid testing of many alternative hypotheses. The major disadvantages are that the growth of an individual tree cannot be predicted with much reliability, and detailed information on tree shape is lacking (Munro 1974). Examples of distance independent models are those of Shugart and West (1977), Mielke et al. (1978), Phipps (1979), and Shugart and Noble (1981).

Stand models consider the forest stand as the focal point of growth. Therefore, they do not incorporate individual tree data, but utilize and provide average stand information (Grabowski 1981). However, some models produce species frequencies and/or diameter distributions. The major use of forest stand models is in evaluation of management

alternatives of commercial forestry operations. The main advantages of this type of model are their ability to utilize conventional inventory information, their fast computation time, and their simplicity. However, since specific individual tree data are lacking, the actual mechanisms that cause changes within a stand do not appear explicitly (Munro 1974). Examples of forest stand models are those of Moser (1972), Ek (1974), and Johnson and Sharpe (1976).

Munro (1974) and Ek and Dudek (1980b) also differentiate between "empirical" and "analytical" forest growth models. Empirical models emphasize close matching of model output to observed results and data. They generally have good statistical fits, but are limited as to interpolation and extrapolation of results. Analytical, or mechanistic, models concentrate on realistic reproduction of biological processes, and are thus generally constrained by the biological characteristics of the data set used. Contrary to empirical models, they often provide poor statistical fits, but have strong interpolative and extrapolative characteristics.

A noteworthy forest succession model is JABOWA, Version II (Botkin et al. 1971, 1972a,b). JABOWA successfully simulates growth of uneven-aged, mixed-species, hardwood forests, of the type found in the Hubbard Brook Experimental Forest in northern New Hampshire, U.S.A. It is a dynamic and stochastic model, in which changes in the state of the

simulated forest are a function of its present state, plus random components. JABOWA would be classified as an analytical, distance independent, individual tree model under the system of Munro (1974).

The philosophy used in building JABOWA was to use a minimal number of assumptions, and to use the simplest mathematical expression for each factor that was consistent with actual observation (Botkin et al. 1971, 1972a,b). New factors were added only when they were needed to resolve differences between generated and observed results, and when information or data were lacking, simple but reasonable relationships were chosen. Consequently, the assumptions and rationale underlying Version II of JABOWA are relatively general, and the builders of JABOWA contend that the model can be applied to other forest regions, and have encouraged this (Botkin et al. 1972a).

A. PURPOSE AND OBJECTIVES

Purpose of Project

The purpose of this study was to modify Version II of JABOWA (Botkin et al. 1971, 1972a,b) so that it could be applied to the boreal forests of Alberta.

Limitations

1. As a variety of forest types exist within the boreal forests of Alberta (Rowe 1972), the modified model applies primarily to the mixedwood section of the boreal forest (Section B.18a of Rowe 1972).
2. The model applies only to mesic upland sites. Version II of JABOWA was designed for situations where moisture is not a limiting factor (Botkin et al. 1971, 1972a,b), and to apply it to hydric or xeric sites would require modifications to the underlying assumptions and structure that were beyond the scope of the project.

Justification

1. Existing growth models for the Alberta boreal forest tend to be empirical stand models. JABOWA is a biologically-constrained analytical model, and the nature and output of the model allow its application to topics relating to forest management (Botkin et al. 1972a). If JABOWA was applied to the boreal forest, the resulting model could provide improved or additional answers to questions relating to forest management concepts and practices.
2. Due to its analytical nature, JABOWA could also be a useful tool in studies of an ecological nature. Many of the mechanisms and processes underlying succession in plant communities have not been elucidated, mainly because of a lack of detailed and conclusive

quantitative data (Drury and Nisbet 1973; Connell and Slatyer 1977). There is a definite lack of data for boreal communities (Larsen 1980). A project such as the one carried out here could support existing knowledge on successional processes, or provide additional insights into them.

Justification for Choosing JABOWA

I encountered success in using a copy of Version II of JABOWA to, in a very general manner, simulate succession in the Alberta boreal forest. Encouraged by this, a more extensive and detailed application was undertaken. Other factors influencing the decision to undertake such a project were:

1. JABOWA is an individual tree growth model, and allows the observation of the behavior of single trees in detail. This is especially useful when considering the effects of management practices and treatments, or ecological phenomena such as competition, suppression, or release.
2. General models such as JABOWA are more suitable for application to other forest regions than models that are restricted to even-aged and/or single-species ecosystems, and to short-term projections (Ek and Dudek 1980a,b; Reed 1980; Shugart and West 1980). In addition, the relatively simple structure of JABOWA does not require extensive data for construction or modification

of the model, and these data can often be of a general nature (Botkin et al. 1972a; Reed 1980).

Objectives

To develop a forest growth model for upland mesic mixedwood sites in the Alberta boreal forest, based on JABOWA (Version II), to:

1. Accurately simulate, during succession, for each species used:
 - a. pattern of basal area accumulation
 - b. pattern of diameter growth
 - c. frequency and diameter distribution
2. Generate trends of living biomass accumulation, and discuss the implications of the results on productivity of forest ecosystems.
3. Use the model to address a number of practical and theoretical management-oriented applications. Due to the wide variety of topics that could be considered, these applications were restricted to silvicultural treatments.
4. Relate the predictions of the model, in conjunction with an analysis of model structure, to existing theories regarding ecological processes and mechanisms that result in species sequences during succession.

The resulting model is called JABOR. This utilizes the first four letters of "JABOWA", and the first three letters of "boreal".

II. LITERATURE REVIEWS

A. ACCUMULATION OF LIVING BIOMASS IN FOREST ECOSYSTEMS

Interest in studies of biomass and dry matter production in forest ecosystems has increased in recent years. Information from these studies can be applied to such areas as ecosystem dynamics, quantitative ecology, complete-tree utilization, and tree nutrition (Doucet et al. 1976). Also, since estimates of biomass can be used to appraise quantities of forest fuel, such estimates can be used to describe flammability of individual trees, tree parts, or tree species (Brown, 1978). Two contrasting models of living biomass accumulation are currently being put forth.

Asymptotic Model

A widely accepted model of productivity of plant ecosystems (Odum 1971; Whittaker 1975) states that accumulation of living biomass during succession is characterized by an asymptotic curve which reaches a maximum at the climax stage. More specifically, in the early stages of succession the rate of total community photosynthesis (P) is greater than the rate of total community respiration (R). Therefore, organic matter, in the form of standing biomass, will accumulate. As succession proceeds, and life strategies emphasize slower rates of growth, and storage of organic

matter that provide long-lasting dominance and protection against physical stress, the P/R ratio approaches a value of one. When the climax stage is reached, the P/R ratio will begin to fluctuate around unity. The magnitude of these fluctuations will be relatively small. These relationships are illustrated in Figure 1.

Whittaker (1975) stated that the asymptotic model can be applied to forest ecosystems. Odum (1971) indicated that the P/R ratio should be an excellent functional index of the relative maturity of an ecosystem or community. The asymptotic model can also apply to accumulation of total (living plus dead) biomass (Odum 1971; Whittaker 1975).

Shifting-Mosaic Model

1. Description

Recently, Bormann and Likens (1979a,b) proposed an alternative model of living biomass accumulation. This model is based on studies at the Hubbard Brook Experimental Forest, and long-term predictions of JABOWA (Botkin et al. 1971, 1972a,b). The model, which will be referred to as the Shifting-Mosaic model, consists of several stages, discussed below in order of their appearance.

a. Aggradation Phase:

Following a major disturbance, such as clear-cutting, net primary productivity increases rapidly in response to increased resource availability, and living biomass accumulates. Productivity rates initially remain relatively

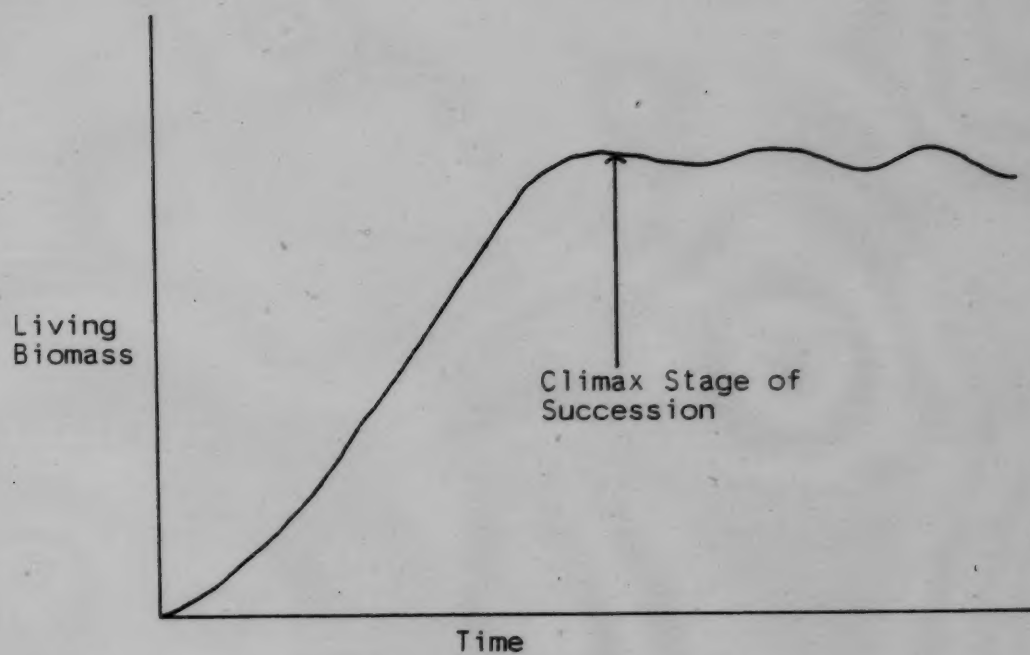


Figure 1. Living biomass accumulation with time, Asymptotic Curve Model

high, as species continue to be characterized by rapid rates of growth. As the transition to dominance by longer-lived, slower-growing species occurs, the rate of productivity declines, but shows a modest and constant excess over death and maintenance rates. This produces a net accumulation of living biomass, which is stored primarily as wood in trees.

As clear-cutting imposes an even-aged condition on the ecosystem, the behavior of most patches or plots within the ecosystem will be synchronous. With the passage of time, thinning occurs on most plots, causing the density of dominants to decline. The plots come to be occupied by fewer and larger even-aged trees dating back to the clear-cut, and a point is reached where the majority of the plots support only one or a few massive trees. At this time, maximum biomass for the developmental sequence is attained. In the northern hardwood forest,¹ this condition occurs at about 170 years.

b. Transition Phase:

As the large, even-aged dominants die out and are replaced by younger trees, there is a period of decline of living biomass on each plot. This causes an overall decline in the living biomass of the ecosystem, as the much lower weights of the individual plots are averaged into the whole. This phase can be thought of as a random opening of the

¹To ensure consistency with the published literature, the phrase "northern hardwood forest" here refers to the forest ecosystem occurring in the northeastern United States, and specifically, in the Hubbard Brook Experimental Forest of New Hampshire.

forest, in which plots become more asynchronous and uneven-aged. Due to the random nature of the process, the Transition Phase will be of variable length of time.

c. Shifting-Mosaic Steady State Phase:

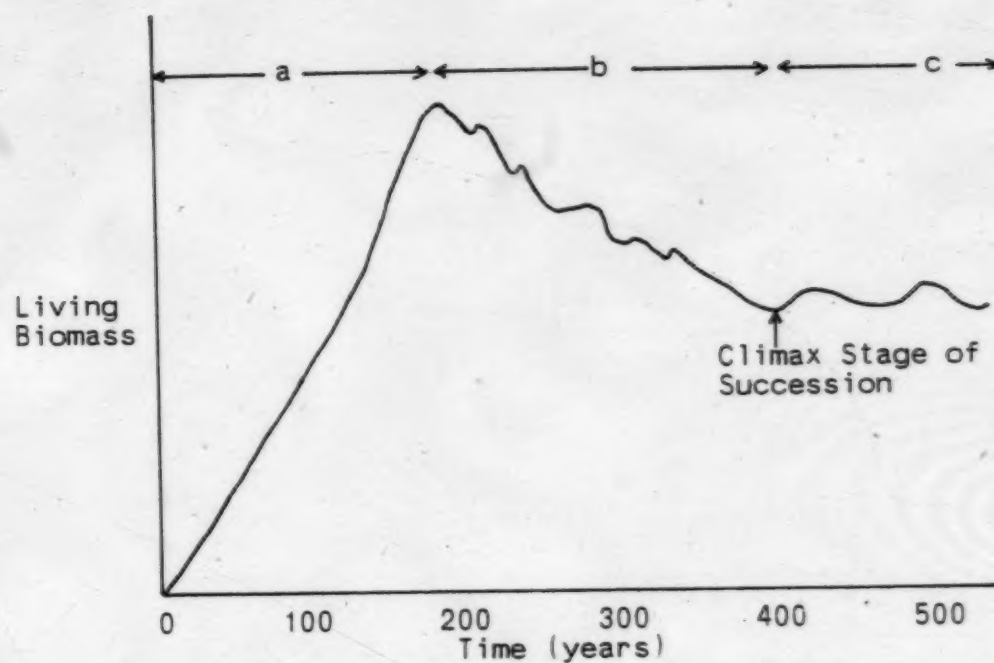
After the progressive elimination of the old even-aged dominants, and with the development of a more or less constant distribution of uneven-aged dominants on the plots throughout the ecosystem, the steady state or climax condition is reached. The proportion of plots in any one stage of development remains more or less constant over time, even though the state of any individual plot may be changing. Bormann and Likens (1979a,b) call this the Shifting-Mosaic Steady State Phase, and based on the JABOWA predictions, propose that it is achieved several centuries after clear-cutting.

Over the long-term, living biomass accumulation shows no net changes. For the ecosystem as a whole, the proportion of plots showing a loss of biomass, through death of individuals or respiration exceeding photosynthesis, balances those showing a gain. As a result, living biomass oscillates irregularly about a mean.

Figure 2 illustrates living biomass accumulation through all phases of the Shifting-Mosaic model.

2. Validation

The basic ideas underlying the Shifting-Mosaic model of living biomass accumulation were first derived from studying the results of JABOWA. Runs for 100 study plots yielded the



a=Aggradation Phase
b=Transition Phase
c=Shifting-Mosaic Steady State Phase

Figure 2. Living biomass accumulation with time, Shifting-Mosaic Steady State Model (from Bormann and Likens 1979a).

same pattern every time, even though the magnitude of the peak and mean biomass values varied, as did the time needed to descend from the peak to the steady state. In evaluating the JABOWA projections, Bormann and Likens (1979a) applied dimension-analysis regression equations (Whittaker et al. 1974) to data from a number of other present-day northern hardwood forests ((Chittenden 1905; Siccama 1974; H. Art, W. Leak, personal communications) cited in Bormann and Likens 1979a), and found that living biomass accumulation in these studies followed their model reasonably well. Bormann and Likens point to these results, and similarities in the results of other studies (Watt 1947; Stearns 1949; Davis 1966; Loucks 1970; Sprugel 1976) as corroborative evidence for their Shifting-Mosaic model.

3. Implications

Bormann and Likens (1979a) proposed that living biomass accumulation is intimately related to the changing dynamics of the whole ecosystem, and that their model provides the basis on which to build an integrated picture of ecosystem development. They contend that their model, and the conditions underlying it, lead to conclusions about ecological processes, energetics, structure, and stability of the northern hardwood forest ecosystem that are quite different from those arising from the asymptotic model. Finally, they propose that the idea of peak living biomass prior to the steady state phase may have wide applicability to other forest ecosystems.

4. Further Developments

Recently, trends of living biomass accumulation similar to those predicted by JABOWA and the Shifting-Mosaic model have been generated by other ecologically-based forest growth models (Shugart and West 1977; Mielke et al. 1978; Phipps 1979; Tharp 1979; Doyle 1981; Shugart and Noble 1981; Shugart et al. 1981). The models of Shugart and West (1977) and Mielke et al. (1978) are adaptations of JABOWA (Ek and Dudek 1980b), and the rest are similar to JABOWA in their form and underlying assumptions (Shugart and West 1981).

B. SPECIES SEQUENCES DURING SUCCESSION

The mechanisms and processes that result in species sequences during succession in plant ecosystems are not well understood. Most studies in the past have been limited to short-term or "single point in time" observations, as only in the last four decades have researchers begun incorporating permanent sample plot bases into their experimental designs (Ek and Dudek 1980b). Most successional sequences persist longer than the usual scientific investigation, and in many cases, later stages have not been directly observed and recorded (Connell and Slatyer 1977). Consequently, detailed and quantitative data are not available for most ecosystems and communities (Drury and Nisbet 1973). An important consequence of this lack of relevant data is that various theories have been proposed concerning the mechanisms and processes underlying changes

in species composition. This literature review discusses the most common and widely-accepted theories.

Historical Review and Development of Classical Theory

Most eighteenth and nineteenth century studies of succession were limited mainly to descriptions of zones and sequences of vegetation. Cowles (1899, 1901) was the first to formulate a general theory for the ecological processes involved. From his studies of sand dunes on the shores of Lake Michigan, Cowles hypothesized that the successions he observed proceeded toward a mesophytic forest, with each stage of vegetation preparing the site for the stage following it.

Clements (1916, 1920, 1928) developed Cowles' (1899, 1901) ideas further, and put forth an elaborate basis for succession. Clements recognized a few great vegetation communities in the world, which he called formations, and said that all plant communities within each formation developed toward a single mesophytic climax association. From this "monoclimax" theory, Clements concluded that a plant community was a discrete taxonomic unit. Clements also saw the interactions between vegetation and habitat as being directive to the highest degree. Although succession was initiated by physical forces, the effect which vegetation exerted upon the habitat was the dominant factor. Species sequences were an orderly process of a plant community changing and irrevocably modifying the habitat, thereby

allowing the community of the next stage to develop. This continued until the community developed to the climax association of the formation, and was characterized by maximum stability, complexity, and organization. In the event of disturbance, succession repeated itself.

The first major revision to Clements' (1916, 1920, 1928) works was the polyclimax theory (Nichols 1923; Cooper 1926), in which the role of site or habitat in succession was emphasized. In a given formation, succession would develop to a mosaic of steady state climax communities, with each community consisting of the species combination best suited to the regional climate and/or physiography. The deterministic nature of Clements' theories was retained, and plant communities were still recognized as discrete units.

Subsequently, North American ecologists studying succession subscribed mainly to the polyclimax theory, or variations of it (e. g. Braun 1950; Dansereau 1957; Odum 1959; Daubenmire 1968). During the last three decades, ecological studies have focused on developing a general theory of the structural and functional characteristics of natural communities (Hutchinson 1957, 1965; Levins 1968; MacArthur 1972; see review by Drury and Nisbet 1973). The deterministic or classical model in its present form is summarized in a review by Connell and Slatyer (1977):

1. A disturbance opens a relatively large space, releasing resources. Of those species that arrive, only certain "early successional" species are adapted for establishment and growth in the conditions that prevail.

2. The early occupants modify the environment, making it less suitable for subsequent recruitment of early successional species. The growth to maturity of later successional species is facilitated by, and dependent upon, these environmental modifications.
3. Earlier species will be eliminated through competition for resources with later species.
4. The sequence continues until the resident species no longer facilitate the invasion and growth of other species.

Odum (1971: 251) stressed that succession is "... an orderly process of community development that is reasonably directional, and therefore, predictable...", and is controlled by the modifications exerted upon the habitat by the vegetation, even though the habitat often determines the rate and extent of development. Whittaker (1975: 146) stated that "The end-point of succession is a climax community of relatively stable species composition and steady state function..."

Contemporary Theory

In recent years, the classical model of succession has come under increasing criticism (McCormick 1968; Connell 1972; Colinvaux 1973; Drury and Nisbet 1973; Horn 1974, 1975; Connell and Slatyer 1977). To many critics, the model is based on unproven analogy and logic, and circumstantial and non-quantitative evidence. As a result, it is not seen as applicable to real systems (Connell and Slatyer 1977). It is viewed as too deterministic, and as depending heavily upon transference of the mechanisms of spatial sequences to

temporal sequences (Colinvaux 1973). While it is felt that the model could be applicable to initial stages of certain primary and secondary successions where extreme environmental conditions must be ameliorated before most plant species can invade (Colinvaux 1973), several studies contradict even this (Drury 1956; Heinselman 1963, 1970; Walker 1970).

The critics of the classical model of succession have not reached agreement on one alternative model. However, there is much accord on many of the principles and mechanisms thought to produce species sequences during succession, and these are summarized in the following discussion.

In contemporary theory, much of the phenomena of succession are seen as the result of the existence of different life strategies (Colinvaux 1973; Drury and Nisbet 1973; Connell and Slatyer 1977; Bormann and Likens 1979a). Many studies indicate that almost all species that appear during a successional sequence will establish as succession starts, or within the first few years, and that this initial floristic composition will be predominantly derived from species present in one form or another in the intact or pre-disturbance community (Egler 1954; Drury and Nisbet 1973; Bormann and Likens 1979a). Species² with opportunistic (Colinvaux 1973) life strategies tend to stand a better

²In this discussion, "species" can be used synonymously with "species group" This is due to the wide variability that can occur in natural systems, and is used for the sake of convenience.

chance of dominating a site in the early stages, as their adaptations include reproduction in vast quantities, wide dispersal of propagules, the ability to remain as dormant biomass for long periods of time, prolific establishment when invading a site or when released from suppression, and rapid growth rates (Colinvaux 1973; Bormann and Likens 1979a). However, these opportunistic species also tend to be relatively shorter-lived, and are unable to grow and reproduce well under strong competition for available resources (Connell and Slatyer 1977). Therefore, even though opportunistic species achieve temporary dominance, they will ultimately surrender the site to longer-lived, more competitive species.

During the earlier stages of succession, the slower-growing and less abundant conservative (Colinvaux 1973) species are suppressed. However, their high tolerance to stress and longer life-spans allow them to survive these long periods of suppression, and to maintain space once they have secured it (Connell and Slatyer 1977). As increasing numbers of the less vagile propagules of the conservative species reach a site, individuals of these species will gradually accumulate (Colinvaux 1973). Many conservative species are adapted to ensure their survival and propagation in the community, through large or massive structures and storage organs that provide protection against physical stress, and through reproductive strategies geared for establishment in an environment where little spare energy is

available. Barring disturbance, succession continues until the tallest and largest of the longest-lived species accumulates relatively more individuals than any other species, and grows into the uppermost position in the canopy (Egler 1954; Connell and Slatyer 1977).

At this point, the existing community correlates to the climax community of the classical model. In modern usage, "climax" is interpreted as the community that, on the whole, is more or less functionally and structurally stable, even though specific points may be undergoing changes of varying magnitude (Horn 1974; Bormann and Likens 1979a; Spurr and Barnes 1980). Changes in species composition, if any, will be gradual.

During succession, structural changes in the community become more pronounced, and tend to enhance the suppression or elimination of earlier species. For example, increased height of plants causes increased shading, and increased size of plants reduces available space. Although the once-dominant earlier species become suppressed or eliminated, most will persist in one form or another, for a number of reasons. Many species have wide ecological amplitudes and can persist through many stages (Drury and Nisbet 1973), and some can remain for long periods as dormant biomass (Bormann and Likens 1979a). Also, as the overall size of the individuals of conservative species increases, the gaps created by the deaths of such individuals will become larger, and this increases the

chances for the growth and survival of vagile intolerant and midtolerant species. Some authors postulate that due to this process, late successional and climax communities may be patchworks of successional stages (Horn 1974; Bormann and Likens 1979a; Spurr and Barnes 1980). Horn (1974) and Spurr and Barnes (1980) stated that such mosaics contribute greatly to the relative instability of climax communities.

Considering the sequences and mechanisms discussed here, modern researchers are hypothesizing that succession is not necessarily a process of continuous change in the species composition of a community, but one of shifting stages of dominance, or relative abundance, of species, species groups, or life-forms (Colinvaux 1973; Drury and Nisbet 1973; Connell and Slatyer 1977). Any appearance of orderly replacement is the visual or overt expression of sequential conspicuousness, reflecting different life strategies (Drury and Nisbet 1973).

Contemporary successional theory cites much evidence indicating that species sequences for a given habitat or community are not necessarily predictable or unidirectional. In most ecosystems, external disturbances tend to occur on a shorter time-scale than that required for a succession to fully develop on an internal basis (Connell and Slatyer 1977). These disturbances can occur on a continuum of degrees and intensities, with varying effects on the ensuing successions. Examples of major external disturbances are fire, logging, agriculture, extensive windthrow, massive

erosion and/or deposition, and disease and insect infestations.

Underlying all of the mechanisms and factors that influence succession are random and stochastic elements. Horn (1974) stated that many of the patterns of succession are direct consequences of stochastic replacements of one plant by another, depending upon such factors as availability of space, supply of propagules, and proximity of propagules to an opening. Bormann and Likens (1979a) stated that disturbances are basically stochastic events.

Particular species are not necessarily relegated to dominance or appearance in certain stages, or to appearance with certain other species or life-forms (Colinvaux 1973; Drury and Nisbet 1973). Under conditions where a species can dominate a site ahead of when it characteristically does so, or an outside species can invade and dominate, some successional stages can be omitted or extra ones added (Gleason 1926; McCormick 1968; Drury and Nisbet 1973; Niering and Goodwin 1974). Successional stages can be delayed or omitted as dominant species inhibit invasion of other species, and/or suppress the growth of those present, through monopolization of space and resources, or habitat modification (Niering and Egler 1955; Westman 1968; Niering and Goodwin 1974). Delays in immigration of invading species can also cause omission or delaying of stages.

In general terms, secondary succession in plant communities is seen as a process that progresses toward

re-establishment of a reasonable facsimile of the community present before disturbance (Drury and Nisbet 1973; Horn 1974, 1975; Bormann and Likens 1979a). The degree of unidirectionality or predictability that occurs depends mainly upon the extent to which the disturbance affects the habitat, the number of species available, the extent of carry-over of species from the pre-disturbance to post-disturbance communities, and the role of stochastic factors (Drury and Nisbet 1973).

III. DESCRIPTION OF JABOWA

A. BASIC MODEL STRUCTURE AND PARAMETERS

JABOWA was built using a step-by-step approach, starting with a species-specific optimal growth rate equation for single trees. The effects of non-optimal levels of light and temperature were added, and then an indirect index of the effects of soil quality. Species strategies arise from different survival probabilities, and differential addition of saplings to the plot, depending on available light on the forest floor and a degree of randomness. The model assumes identical and unchanging genetic properties for all individuals of a species, and constant climatic conditions. It considers all model species that can grow on a site as part of the available reservoir for entry into the stand, and does not take species migration into account. For these reasons, the builders of JABOWA stated that long-term predictions of the model must be treated with caution (Botkin et al. 1972b).

The tree species used in JABOWA, divided by tolerance (Spurr and Barnes 1980) classes are:

1. tolerant: beech (*Fagus grandifolia* Ehrh.), white ash (*Fraxinus americana* L.), mountain ash (*Sorbus americana* Marsh.), sugar maple (*Acer saccharum* Marsh.), mountain maple (*A. spicatum* Lam.), striped maple (*A. pennsylvanicum* L.), red maple (*A. rubrum* L.), balsam fir

(*Abies balsamea* (L.) Mill.), red spruce (*Picea rubens* Sarg.)

2. intermediate: yellow birch (*Betula alleghaniensis* Britton), white birch (*B. papyrifera* Marsh.)
3. intolerant: pin cherry (*Prunus pensylvanica* L. f.), choke cherry (*P. virginiana* L.)

These tree species were characterized by the following biotic parameters:

1. maximum observed age, height, and diameter
2. a soil moisture range for growth
3. number of saplings that can enter a plot
4. relationships between:
 - height and diameter
 - leaf weight and diameter
 - rate of photosynthesis and available light
 - rate of photosynthesis and a measure of climate

Data from the entire geographical range of each species were used.

Description of the abiotic environment was limited to features that have been recorded for 208 plots in the Hubbard Brook Experimental Forest (Bormann et al. 1970). The parameters used are:

1. plot elevation
2. soil depth and water-holding capacity
3. percentage of soil that is rock
4. a measure of annual insolation above the forest canopy
5. average monthly temperature and precipitation values,

recorded at a weather station in the Hubbard Brook Experimental Forest

Output of JABOWA consists of species frequencies and total number of trees on 100 m² (10 m x 10 m) plots, diameter at breast height (DBH) of each tree, basal area per species and total plot basal area; and living biomass on the plot, per tree component. The program is interactive, and is very flexible in allowing manipulation of the stands being simulated. The user may alter environmental factors, and any factors or events that can be expressed as a change in species growth rates, or birth and/or mortality rates. The user can also specify values for output variables such as output interval, length of simulation run, and number of runs for a given plot.

Subsequent versions of JABOWA have included work on incorporating water, mineral, and energy cycling, and volume calculation. The results of these improvements have not been widely disseminated.

B. GENERAL DESCRIPTION OF PROGRAM AND FUNCTIONAL RELATIONSHIPS

This section discusses only the major functional relationships of Version II of JABOWA. A flow chart of the program, and a brief description of each subroutine, are included in Appendix I.

1. Calculation of site characteristics:

The abiotic program parameters are used to calculate indices

of climate and available soil moisture.

- a. The climatic index incorporates the effects of temperature, and is based on a growing degree-day value (40°F) for the plot. The program equation utilizes average monthly temperature values for July and January, which are corrected by lapse rates to account for differences between the elevations of the plot and the weather station. This equation gives a sinusoidal fit to the average July and January temperatures.
- b. Available soil moisture is based on actual evapotranspiration values, which are calculated from a modified Thornthwaite water balance equation.

2. Introduction of trees to plot:

Trees are stochastically introduced to the plots, to simulate the random factors involved in tree reproduction. To avoid calculation of seed viability rates, and germination and mortality probabilities, trees are introduced as saplings, at a DBH of 0.5 cm plus a random addition of up to 0.3 cm.

It is assumed that there is a seed source available for each species. However, only those species that can grow on the plot are added. This is determined by plot openness, and site conditions of growing degree-days and actual evapotranspiration.

The following procedure is used:

- a. Plot openness is calculated, based on leaf weight for the plot, by the equation:

$$WT = \sum C(i) \times D(m)^2$$

where:

- i. $C(i)$ is a species-specific leaf area constant, in gm/cm^2
 - ii. D is diameter at breast height in cm of tree m
- Since leaf area is assumed to be proportional to leaf weight, it is felt that this equation gives a good approximation of the degree of shading on the plot.
- b. The plot degree-day and actual evapotranspiration values are checked against the minimum and maximum values of each species. All species that cannot grow under the site conditions are eliminated.
 - c. It is assumed that all of the tolerant species can survive under all conditions of stand openness. For each year, one tolerant species is randomly chosen, and 0, 1, or 2 saplings of that species are added to the plot.
 - d. If plot leaf weight does not exceed the default weight for the survival of the intolerant cherry species, pin cherry or choke cherry saplings are randomly added to the plot. Where the ranges of the two species overlap, one is chosen randomly, with the choice weighted by a species distribution constant.
 - e. If plot leaf weight does not exceed the default weight for the survival of the intermediate birch species, white or yellow birch saplings are randomly introduced, with the number added weighted by stand density. Where the ranges of the two species overlap, one is chosen

randomly, with the choice weighted by site and species constants.

3. Calculation of diameter growth of trees:

Diameter growth of each tree on the plot is calculated deterministically. Botkin et al. (1972a) stated that the amount of radiant energy that a tree growing in the open receives is roughly proportional to its leaf area. They also stated that under optimal conditions, the change in volume of a tree over a period of one year is proportional to the amount of sunlight received, derated by the energy required to maintain the living tissue. This can be expressed by the equation:

$$\Delta \text{volume} = \Delta D^2 H = K \times LA \times (1 - DH / (DBHMAX \times HTMAX))$$

where:

- a. D is the DBH of the tree, in cm
- b. H is height in cm, calculated by:

$$H = 137 + b_2 D - b_3 D^2$$

where b_2 and b_3 are constants, calculated by:

$$b_2 = 2(HTMAX - 137) / DBHMAX$$

$$b_3 = (HTMAX - 137) / DBHMAX^2$$

and HTMAX, and DBHMAX are, respectively, maximum attainable height and maximum attainable diameter for the species

- c. K is a constant
- d. LA is the leaf area of the tree, calculated by:

$$LA = C(i) \times D^2$$

- e. The factor $(1 - DH / (DBHMAX \times HTMAX))$ represents the energy

cost of maintenance.

Utilizing the assumption that leaf area is proportional to leaf weight, Botkin et al. (1972a) defined a species-specific growth rate constant, $G(f)$, equal to $k \times C(f)$. The growth rate equation could then be rewritten in terms of diameter growth. As this equation calculated growth under optimal environmental conditions, factors were added that allowed for the effects of shading, climate, and soil quality. The final equation derived was:

$$\Delta D = G(f)D \times \frac{(1-DH/(DBHMAX \times HTMAX))}{(274+3b2D-4b3D^2)} \times R(AL) \times T(DEGD) \times S(BAR)$$

where:

- a. $R(AL)$ is the factor representing the effects of shading, shade tolerance, and site insolation, and is calculated by:

$$\text{Tolerant species: } R(AL) = 1 - \exp(-4.64(AL - 0.05))$$

$$\text{Intolerant species: } R(AL) = 2.24(1 - \exp(-1.136(AL - 0.08)))$$

where AL is the light available to each tree, calculated by:

$$AL = PHI \times (\exp(-k \cdot SLA))$$

where:

- i. SLA is shading leaf area, and is calculated by summing the leaf weights of all trees taller than the one being considered
- ii. PHI is the relative light level above the tree canopy, and has a default value of 1.0
- iii. k is a constant, adjusted for reasonable shading

beneath a dense canopy; value=1/6000.

R(AL) varies between 0 and 0.99 for tolerant species, and between 0 and 1.45 for intolerant species.

- b. T(DEGD) is a species-specific factor representing climatological effects, and is calculated by

$$T(DEGD) = \frac{4(DEGD-DMIN)(DMAX-DEGD)}{\pi(DMAX-DMIN)^2}$$

where DMIN and DMAX are, respectively, minimum and maximum growing degree-day values for each species, obtained from maps, and DEGD is the growing degree-day value for the plot, determined in calculation of site characteristics.

This function is a parabola, with the value zero at minimum and maximum values of DEGD, and a value between zero and one for any values of DEGD between these limits.

- c. S(BAR) is an expression representing the effects of competition for soil moisture and nutrients, and is calculated by:

$$S(BAR) = 1 - BAR/SOILQ$$

where BAR is the total basal area on the plot,

and SOILQ is the maximum basal area the plot can support.

S(BAR) varies between 0 and 1, depending on basal area present on the plot.

The growth rate equation used in JABOWA results in an S-shaped growth curve for individual trees, as shown in

Figure 3.

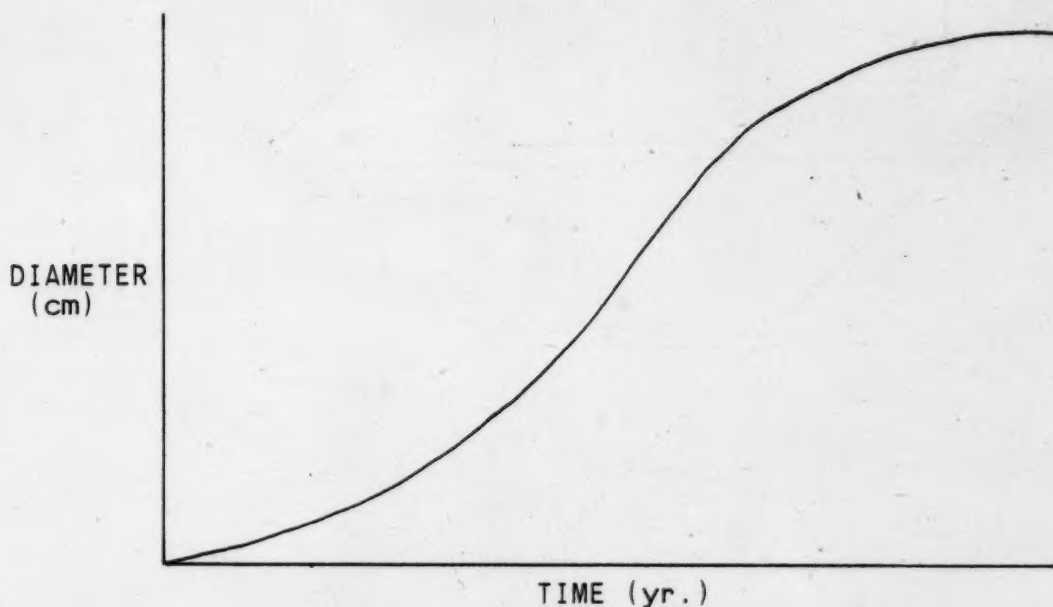


Figure 3. Time-dependent solution of the diameter growth rate equation used in JABOWA (Version II)

4. Tree mortality:

Trees are stochastically removed from the stand by two separate mechanisms, to simulate death of trees.

a. Age-independent death: It is assumed that for actively growing trees, only 2% should reach the maximum age for the species. This results in the probability that a tree will die in any given year of

$$p = 1 - (1 - E)^n$$

If E is defined as the death probability, p set equal to 0.98, and n set equal to the maximum attainable age of the species being considered, $AGEMX(i)$, the above equation can be approximated by:

$$E=4.0/AGEMX(i)$$

For each species present on the plot, a value for E is calculated. For each tree on the plot, a random number between 0 and 1, R , is generated. If R is less than the appropriate E , the tree is removed.

The rationale used is that numerous events, such as insect or disease infestation, severe wind, lightning, etc., may result in the death of a tree at any time. While only some of these events are truly random, the sum of the effects of all possible causes of death approaches a random probability of killing any tree in any year (Botkin et al. 1972a).

b. Growth-dependent mortality: This mechanism simulates death by suppression. If the last diameter increment (DINC) of a given tree is less than the species-specific minimum value for active growth (AINC, equals 0.01 cm for all species in JABOWA), that tree is added to a vector called NOGRO. It is assumed that any tree added to the NOGRO vector for ten consecutive years should not have more than a one per cent chance of surviving those ten years. Therefore, the probability that such a tree will die in any one year is 0.368. For any tree with DINC less than AINC, a random number between 0 and 1 is generated, and if that number is less than 0.368, the tree is removed.

The default value of AINC can be changed by the user.

C. RESULTS AND VALIDATION

To evaluate the predictions of JABOWA, averaged results from multiple runs of the model were compared to actual data for the Hubbard Brook Experimental Forest (Bormann et al. 1970; Chittenden 1905, cited in Botkin et al. 1972b) and data for other northern hardwood forests (Bormann and Buell 1964; Loucks 1970; Siccama 1968 and Marquis 1969b, cited in Botkin et al. 1972b). Difficulty was encountered in direct comparison between the Hubbard Brook and simulated plots, as the actual plots varied considerably in environmental conditions, and the forest has a somewhat complicated and poorly documented history. Despite this, the optimal simulated plots showed characteristics very similar to a large number of actual plots, and JABOWA was judged to be successful in reproducing tree species succession for the northern hardwood forest (Botkin et al. 1971, 1972a,b).

D. LIMITATIONS AND WEAKNESSES

The major difficulty encountered in all aspects of construction and validation of JABOWA was in obtaining relevant and reliable data (Botkin et al. 1972a,b). Data on species characteristics, especially those dealing with birth, growth, and mortality, were particularly limiting (Botkin et al. 1972a,b). This often necessitated usage of over-simplified assumptions and mathematical expressions, which caused biasing of results. For example, the random introduction of tolerant species may underemphasize the

importance of major species such as beech, and overemphasize the importance of minor species such as red maple (Botkin et al. 1972b). However, biasing of species entrance requires further field study. Also, the number of cherry saplings that can be introduced to a plot is far below what is actually observed. To balance this, the cherries are given a higher probability of survival than is observed, and realistic numbers are obtained by about year 10. In stands 50 to 60 years old, there is overestimation at certain elevations of total number of stems, and number of stems in several diameter classes. These inaccuracies are caused mostly by a biasing of the model predictions towards the birch species in the first 50 to 60 years of most simulation runs. They also involve inaccurate mortality rates, which could be modified with relative ease, if it were not for a lack of verification data (Botkin et al. 1972b).

In a number of cases, distinct anomalies in species composition exist between the actual and simulated plots. Botkin et al. (1971) concluded that these differences resulted from two previous loggings of the Hubbard Brook Experimental Forest (Bormann et al. 1970).

The major weaknesses of Version II of JABOWA are:

1. As JABOWA was designed for sites where moisture is not a limiting factor upon tree growth, the model cannot be used for hydric or xeric sites (Botkin et al. 1972a).
2. The small plot size can cause exaggerations when the results are enlarged to a per hectare basis (B. L.

Phillips, personal communication).³ For example, removal of one large tree can drastically affect basal area for the plot. A solution is to do large numbers of sample runs and obtain averages, but this can be expensive.

3. The effects of neighboring plots are not considered. Therefore, the effects of competition from, or release from competition from, trees adjacent to the plot are not included. This, however, is a feature common to all forest growth models (Shugart and West 1980).
4. Saplings, and not seedlings, are introduced. This is a misrepresentation of actual birth processes.
5. There is only one class of tolerant species. Further differentiation to tolerant and very tolerant would be helpful.
6. The model is not as sensitive to changes in the relationship between photosynthesis and available light as it might be (Botkin et al. 1972a).
7. The relationships between tree diameter and leaf weight, and tree growth and competition for soil moisture and nutrients, should be more precise (Botkin et al. 1972a).

³B. L. Phillips, Assistant Professor, Department of Forest Science, University of Alberta, Edmonton, Alberta.

IV. METHODS

A. BASIS OF THE JABOR MODEL

It was decided, in developing the JABOR model, to employ the same philosophy used in building JABOWA. The model was kept as simple as possible, and changes to the basic assumptions and relationships were made only when needed to improve accuracy and/or realism. Tree species data were collected from the entire North American geographical range of each species, with emphasis on data from Alberta forests whenever problems arose as to accuracy of model predictions.

B. SPECIES USED

The following species were originally considered for use in the model: white spruce (*Picea glauca* (Moench) Voss), black spruce (*Picea mariana* (Mill.) B.S.P), trembling aspen (*Populus tremuloides* Michx.), balsam poplar (*Populus balsamifera* L.), balsam fir, jack pine (*Pinus banksiana* Lamb.), lodgepole pine (*P. contorta* Dougl.), white birch, and tamarack (*Larix laricina* (Du Roi) K. Koch). Black spruce and tamarack were initially rejected, because although they occur on boreal upland mesic sites, they are most common on wetter sites. A wealth of literature supports this observation. Lodgepole pine was also eliminated, as its range does not extend past central Alberta, and it is more

typical of subalpine forests (Fowells 1965, Hosie 1973). During data collection, white birch, jack pine, and balsam poplar were also rejected. Although these species occur commonly on upland mixedwood sites,⁴ they tend to be minor constituents. There is also a lack of relevant data for them. Consequently, it would be difficult to accurately simulate the behavior of such species in an analytical forest growth model.

A sufficient amount of accurate data were obtained for program parameters for balsam fir. However, difficulties arose when determining how to simulate the behavior of this species, and it was eliminated from the model. The most problematic areas were the mechanisms and timing of the entrance of balsam fir, and the nature of the interactions between it and white spruce. Further difficulty was encountered in that the validation data that were used contained gaps as to when the actual introduction of balsam fir occurs. As these information shortages would cause difficulties in accurately simulating the behavior of balsam fir in an analytical growth model, the species was eliminated from the model.

After elimination of the above species, white spruce and trembling aspen remained. Data collected for species eliminated from the model can be obtained by contacting Dr.

⁴Except where more specificity is required, the term "upland" is interchangeable with "mesic upland", and "mixedwood" is interchangeable with "western Canadian mixedwood boreal". This is for the sake of clarity and consistency.

K. O. Higginbotham or Professor B. L. Phillips, of the Department of Science, University of Alberta.

C. OVERVIEW OF METHODOLOGY

Discussion of the data and parameters collected will depart from the actual methodology used. The actual sequence of steps was as follows:

1. Literature search to obtain data for program parameters and functions. The parameters and functions used corresponded exactly to those used in Version II of JABOWA. Values for parameters derived from data collected were also calculated.
2. Insertion of data collected into program, with appropriate changes to program coding and algorithms.
3. Validation data collection.
4. Trial runs of program to produce preliminary results for comparison to validation data.
5. Adjustment of program parameters, plus modification of program assumptions and functions, to increase accuracy of results.
6. Fine tuning of results to validation data, based on multiple program runs.

In this discussion, separate treatment is given to data collected for environmental parameters and functions, and for tree species parameters and functions. In each case, initial, and if applicable, final, values for program parameters are presented first. Methodology, and all changes

to program assumptions and functions, are then dealt with. Discussion of validation data collection, and validation procedures and obtaining of results, follows.

A source listing of the program, a sample run to year 30, and an index of parameters that can be changed interactively are included in Appendix II.

D. DATA COLLECTION AND PROGRAM CHANGES

Environmental Parameters and Functions

The nature of certain parameters necessitated selecting a representative area or location with the western Canadian boreal forest. Whitecourt, Alberta, was chosen, as there were no gaps or shortages in the data for this area.

Table 1 shows values used for all environmental parameters.

1. Elevation (BASEH), average monthly precipitation (BASEP), average monthly temperature (BASET):

Environment Canada (1982) contains climatic records for the period 1951-1980 for the Whitecourt weather station. Elevation of the weather station is also given.

2. Maximum growing degree-days in the western Canadian boreal forest (DEGD):

Energy, Mines, and Natural Resources (1970) contains 5.5°C (42.0°F) base degree-day values. It was felt that this base temperature could be applicable to tree growth (K. O.

Table 1. Data collected for environmental parameters used in JABOR.

	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
BASET	2.1	13.6	21.4	36.9	48.1	54.9	59.2	57.0	48.0	38.1	20.7	8.4
BASEP	1.15	0.95	0.95	1.06	2.13	3.61	4.00	3.48	1.36	1.09	0.93	1.05
BASEH	741.0											
TILL	10.0											
TEXT	150.0											
EXCESS	25.0											
PHI	1.0											
DEGD	3000.0											
SOILO	20000.0											

BASET: average monthly temperature (°F)
 BASEP: average monthly precipitation (in.)
 BASEH: elevation of the weather station at which the climatic data were recorded (m)
 TILL: average soil depth (m)
 TEXT: average amount of soil available for water storage (mm/m)
 EXCESS: fraction of precipitation available for evapotranspiration (%)
 PHI: relative light level available above the forest canopy (no units)
 DEGD: maximum number of growing degree-days available in the western Canadian boreal forest (5.5 °C base)
 SOILO: maximum basal area a 100 m plot can support (cm²)

Higginbotham, B. L. Phillips, personal communications),⁵ and was acceptable for the purpose of this project. There was close agreement between the 3000 degree-day iso-line and the southern edge of the boreal forest in Manitoba (Rowe 1973).

3. Maximum basal area a 100 m² plot can support (SOILQ):

Maximum basal area for upland mixedwood sites in Alberta was found to be approximately 100 m²/ha (Johnstone 1977; B.L. Phillips, personal communication). Botkin et al. (1972a) stated that the value used for SOILQ in JABOWA, 200 m²/ha, is sufficiently large that halving or doubling it does not significantly affect the results of the model. Considering this, a value of 200 m²/ha (20000 cm²/100 m²) was initially used in JABOR. Further modification was not necessary.

4. Other Environmental Parameters:

Based on the results of the preliminary runs of the model, the JABOWA default values for average soil depth (TILL), average amount of soil available for water storage (TEXT), fraction of precipitation available for evapotranspiration (EXCESS), and relative light level available above the forest canopy (PHI), were used. The first three parameters are used in calculating actual evapotranspiration for the plot, which is used as an index of soil moisture. However, the evapotranspiration value is used only in determining whether a species can be considered for introduction to a site (Botkin et al. 1972a). Therefore, the default values for these variables were considered good approximations of

⁵K. D. Higginbotham, Associate Professor, Department of Forest Science, University of Alberta, Edmonton, Alberta.

the conditions that exist on most upland mixedwood sites. Alteration of the nature of PHI would require substantial modification of the tree growth functions, and it was decided to undertake this only if absolutely necessary.

Tree Species Parameters and Functions

Table 2 contains initial and/or final values for all tree species parameters.

I. INTRODUCTION OF TREES

1. Minimum and maximum growing degree-days required for growth and regeneration (DMIN and DMAX):

a. DMIN: Northern species ranges (Hosie 1973) were super-imposed over 5.5°C base degree-day iso-lines (Energy, Mines, and Natural Resources 1970). Some interpolation was needed in determining DMIN values.

b. DMAX: The southern ranges of white spruce and trembling aspen extend into the United States (Fowells 1965; Hosie 1973). However, as 5.5°C base degree-day values for the United States could not be located in the literature or through individual referrals, estimates of DMAX were derived by following the procedure used by Botkin et al. (1972a) for species in JABOWA. Species ranges (Fowells 1965) were super-imposed over normal January and July daily average temperatures for the United States for the period 1941-1960 (United States Department of Commerce 1968). January and July temperatures were recorded wherever the isotherms of both months crossed the southern limit of a species range at

Table 2. Data collected for tree species parameters used in JABOR.

SPECIES	DBHMAX	HTMAX	AGEMX	DMAX	DMIN	WMAX	WMIN	ITYPE	ASPWT	C	F	G	B2	B3
Sw INITIAL	121.9	56.08	400	3500	750	600	150	2	-	13.0	2.000	119.4	89.8	0.370
Sw FINAL	91.4	33.54	250	3500	750	600	150	2	-	13.0	2.180	122.5	70.4	0.385
Aw INITIAL	114.3	33.54	200	5300	950	600	150	1	400.0	5.0	1.972	147.0	56.3	0.246
Aw FINAL	70.0	27.43	120	5300	950	600	150	1	550.0	5.0	1.900	190.0	74.5	0.532

DBHMAX: maximum attainable DBH (cm)

HTMAX: maximum attainable height (m)

AGEMX: maximum attainable age (yr)

DMIN and DMAX: respectively, minimum and maximum growing degree-days (5.5 C base) required for growth and regeneration

WMIN and WMAX: respectively, minimum and maximum actual evapotranspiration required for growth and regeneration (mm)

ITYPE: shade tolerance (1: intolerant; 2: tolerant)

ASPWT: leaf weight under which the early successional trembling aspen can be introduced to a plot (gm)

C: leaf area constant (gm/cm²)

F: exponential factor added into the equation used for calculating leaf weight;

this factor is discussed in more detail later

G: species-specific growth rate constant (cm/yr)

B2 and B3: species-specific growth constants (no units)

the same place. Outlying pockets of a species were ignored, except for the largest ones. Interpolation was required by this procedure, but was minimized as much as possible. Each set of January and July temperatures was inserted into the formula used in JABOWA for calculating degree-days, and for each species, the largest realistic value of those produced was chosen.

2. Minimum and maximum actual evapotranspiration required for growth and regeneration (WMIN and WMAX):

- a. WMIN: Northern species ranges (Hosie 1973) were super-imposed over evapotranspiration values (Energy, Mines, and Natural Resources 1978). Some interpolation was needed.
- b. WMAX: Actual evapotranspiration values for the United States could not be obtained from the literature or through individual referrals. In JABOWA, only one value of WMAX was used, that being 600 mm for white birch, for the New York City area. As the southern species ranges of white spruce and trembling aspen in this area are reasonably close to that of white birch (Fowells 1965), and this region would experience higher actual evapotranspiration than interior locations, a value of 600 mm was used for both species.

3. Number of individuals of each species that can be added in a single year:

- a. White spruce: The JABOWA birth function for tolerant species, in which 0 to 2 saplings are randomly added per year, was initially retained. The main criterion was that in addition to being very simple, the function is a good

approximation of the reproduction strategies of tolerant species (Drury and Nisbet 1973; Connell and Slatyer 1977).

In preliminary runs, frequencies of white spruce were consistently overestimated, even with alteration of the mortality algorithms. The number of trees that could be randomly added per year was reduced to 0 or 1. Also, the effects of stand density and leaf shading were incorporated, by progressively decreasing the probability of white spruce introduction as leaf weight on the plot increased. This is considered reasonable, for the following reasons:

- i. Although the potential seed source for white spruce will increase as more trees of a seed-bearing age become present, seedbed conditions will often worsen during succession. This is due mainly to increases in litter and deadfall production, and in shading and competition from understory species for space and resources. It is well documented in the literature that white spruce will often establish prolifically on disturbed sites that are free from extensive competition (Jarvis et al. 1966; Larsen 1980).
- ii. Although white spruce is considered a tolerant species, as shading and stand density increase, so does the potential for suppression and death of smaller trees. As trees are introduced as saplings in the model, the argument can be made that more trees are being introduced to a plot than are actually visible, but many of them are dying due to suppression before they reach a height of 1.37 m (breast height).

The procedure used was to establish a number of plot leaf weight ranges, which were given the common label WEIGHT, and respective probability levels of introduction. In the program, a random number between 0 and 1 is generated, and if this number is greater than the probability level for the current leaf weight range, 0 or 1 trees can be introduced. The values for the leaf weight ranges and probability levels were chosen arbitrarily, and adjusted during fine tuning to produce accurate results for species frequencies and basal areas. The final values were:

- i. $\text{WEIGHT} \leq 15.0 \text{ kg}$: $p=0.250$

Where p is the probability level.

Weights of 15.0 kg are usually reached between 35 and 45 years after stand establishment.

- ii. $\text{WEIGHT} > 15.0 \text{ kg}$ and $\leq 65.0 \text{ kg}$: $p=0.450$

Weights of 65.0 kg are usually reached 130 or more years after stand establishment.

- iii. $\text{WEIGHT} > 65.0 \text{ kg}$: $p=0.615$

b. Trembling aspen: The JABOWA function for white birch, which introduces 0 to 13 saplings, based on plot leaf weight, was originally used. The main criterion was that the function was simple, and could be easily manipulated. However, the function introduced all of the trembling aspen within the first four or five years from the start of a run, and the majority within the first two or three years. This resulted in very little variation in diameters, and distinct clumping of aspen as to size as succession proceeded.

Although this function was a good representation of the way additions occur in nature (Bella and DeFrancheschi 1980; Larsen 1980; Grabowski 1981), it resulted in biasing of predicted diameter distributions, and distortion of predicted patterns of basal area and biomass accumulation.

A first step in remedying this problem was to widen the diameter range of saplings at introduction, to include DBH's as low as 0.001 cm and as large as 0.999 cm. This was also done for white spruce. The next steps were to add fewer trees per year by the function based on plot leaf weight, and utilize a function similar to that used for white spruce, in which zero or one saplings is randomly introduced each year. The latter step was necessary because the validation data indicated that in all ages of stands, aspen was usually present in the lower and middle diameter classes, as well as in the higher ones. These trees were, however, generally small in number, especially in older stands.

These steps did not completely solve the problem, and it was decided to initially introduce an even smaller number of aspen each year, and obtain reasonable estimates of total numbers by year ten or fifteen. Since validation data were not available for stands less than 30 years of age, and the literature on aspen frequency in stands younger than 30 years generally deals with pure aspen stands (Kirby et al. 1957; Bella and DeFrancheschi 1980; Grabowski 1981), any predictions of the model for stands less than 30 years old

would have to be treated with caution. Consequently, the significance of any inaccuracies in the first ten to fifteen years is diminished.

The final algorithm used introduced five to nine saplings per year, with the actual number chosen randomly and not biased by plot shading, until the default plot leaf weight for introduction of aspen (ASPWT; see below) was exceeded. This usually occurred at year eight or nine. As well, random additions of zero or one sapling per year occurred throughout the duration of the simulation. Including the effects of mortality, average frequency of trembling aspen for year 10 was about 36 stems per plot, and about 28 stems by year 15. These values are similar to the results of Kirby et al. (1957), Bella and DeFrancheschi (1980), and Grabowski (1981). The ultimate goal in developing this algorithm, however, was obtaining accurate values by year 30, at which point the validation data begin.

The random introduction of saplings overestimated number of aspen in the lower and middle diameter classes in later years. To remedy this, the effects of stand density and leaf shading were incorporated. This is justifiable because as white spruce increases in size and density, and causes increased shading on the forest floor, the ability of aspen to sprout and survive decreases (Jarvis et al. 1966; Dix and Swan 1971; Larsen 1980; Day and Harvey 1981). The procedure used was the same as for white spruce, and the final leaf weight ranges and probability levels chosen were:

- i. WEIGHT $\leq$ 17.0 kg: $p=0.630$

Weights of 17.0 kg are usually reached between 40 and 50 years after stand establishment.

- ii. WEIGHT $>$ 17.0 kg and $\leq$ 30.0 kg: $p=0.825$

Weights of 30.0 kg are usually reached between 60 and 75 years after stand establishment.

- iii. WEIGHT $>$ 30.0 kg: $p=0.970$

4. Leaf weights under which trembling aspen can be introduced to a plot (ASPWT):

As no information regarding leaf weights under which trembling aspen can sprout was readily available, the JABOWA value for white birch was initially used. This value was altered during fine tuning of the model.

II. TREE MORTALITY

1. Maximum attainable age (AGEMX) and size-dependent mortality:

Although overestimation of species frequencies was remedied to an extent by altering the birth functions, an inordinate number of trees were growing to diameters greater than 40 cm, and diameters greater than 60 and 70 cm were occurring much too often. As the AGEMX parameter is used in determining the probability of age-independent death for a species, the AGEMX values obtained (Fowells 1965; Sutton 1969) were altered. This was not an unreasonable procedure because it was noted that the AGEMX values used in JABOWA do not seem representative of the maximum values that could

occur over the entire geographical ranges of the species used. This observation is supported by the fact that Botkin et al. (1972a,b) frequently stated that manipulation of data was required to get a closer fit of simulated to observed results. In addition, although Botkin et al. (1971, 1972a,b) utilized Harlow and Harrar (1941) as their main data source, some of the data cited were lower than those of Harlow and Harrar, and many of the values used in JABOWA were lower than those given by Fowells (1965). Considering these factors, AGEMX values that were reasonable estimates of maximum attainable ages for white spruce and trembling aspen in Alberta were selected.

This step did not completely solve the problem, as there were still too many trees reaching large diameters. Rather than develop new functions for mortality rates, for which very little data exist (Botkin et al. 1972a; Ek and Dudek 1980b; Reed 1980; Shugart and West 1980, 1981), the probability of age-independent mortality was increased at certain diameter limits. While such a step in effect converts this mortality function to an age-dependent or size-dependent mechanism, it can be considered reasonable in that as a tree grows larger and older, the chance of death due to factors such as windthrow, insect or disease infestation, and harvest, increases. The final diameter limits and probability levels used are given in Table 3. These probability levels result in a non-linear function with a slightly convex slope. The somewhat higher

Table 3. Diameter limits and probability levels used in size-dependent mortality function of JABOR.

DBH (cm)	Probability Level	Annual Probability of Death (%)	
		Sw	Aw
≤34.0	Sw: 3.75/AGEMX Aw: 4.25/AGEMX	1.5	3.5
>34.0 and ≤36.0	4.3/AGEMX	1.7	3.6
>36.0 and ≤38.0	4.8/AGEMX	1.9	4.0
>38.0 and ≤40.0	5.3/AGEMX	2.1	4.4
>40.0 and ≤42.0	6.0/AGEMX	2.4	5.0
>42.0 and ≤44.0	7.5/AGEMX	3.0	6.3
>44.0 and ≤46.0	9.0/AGEMX	3.6	7.5
>46.0 and ≤48.0	10.5/AGEMX	4.2	8.8
>48.0 and ≤50.0	12.5/AGEMX	5.0	10.4
>50.0	13.5/AGEMX	5.4	11.3

probability level for trembling aspen than for white spruce at diameters below 34.0 cm was required for accuracy of results.

During fine tuning of the model, the AGEMX value for trembling aspen was lowered slightly.

2. Growth-dependent mortality:

It was also necessary to adjust the growth-dependent mortality functions. In JABOWA, the minimum diameter growth required to avoid eligibility for growth-dependent mortality (AINC) was set at 0.01 cm/yr for all species. This value was not considered appropriate for boreal species, and was increased for use in JABOR. Final values of 0.08 cm for white spruce and 0.10 cm for trembling aspen were used, and were considered reasonable approximations (K.O.Higginbotham, B.L.Phillips, personal communications). In fine tuning, the probability of mortality due to suppression was increased slightly, and the original threshold value of 0.368 was reduced to 0.350. This had very little effect on the actual probability of death, but did bring about an improvement of results.

III. TREE GROWTH

1. DBHMAX and HTMAX:

When the initial values obtained (Sutton 1969; Brinkman and Roe 1975) were incorporated into the growth rate equation, questionable rates and patterns of diameter growth were produced for both species. As well, since tree height is

deterministically calculated from tree diameter in the model, inaccurate height values resulted. It was again noted that DBHMAX and HTMAX values used in JABOWA were often lower than the values of Harlow and Harrar (1941) and Fowells (1965). Therefore, values that were reasonable estimates of maximum attainable diameters and heights for white spruce and trembling aspen in the Alberta boreal forest were chosen. The final values used were based primarily upon Alberta Forest Service (1979) prediction tables (S.J. Titus, personal communication),⁶ the validation data used, height-diameter relationship tables for trembling aspen in Alberta (J. D. Heidt, personal communication),⁷ and tests of various values in the growth rate equation. As the model is not extremely sensitive to changes in DBHMAX and HTMAX (Botkin et al. 1972a), fine tuning of the model did not require alteration of the values chosen.

The values for DBHMAX and HTMAX were used to calculate values for the growth constants b2 and b3.

2. G:

Botkin et al. (1972b) stated that the values of G used in JABOWA were arbitrarily set so that a tree m of species i reaches $2/3$ of DBHMAX(i) at $1/2$ of AGEMX(i). They also included the mathematical procedure used to do this, and this procedure was applied to the data collected for white spruce and trembling aspen. However, there were no reliable

⁶S. J. Titus, Associate Professor, Department of Forest Science, University of Alberta, Edmonton, Alberta.

⁷J. D. Heidt, Associate Professor, Department of Forest Science, University of Alberta, Edmonton, Alberta.

data with which to verify the values obtained. These values were therefore inserted into the program, and adjusted during trial runs and fine tuning.

3. C, F:

Data on the quadratic relationship between leaf weight and DBH that is used in JABOWA, $WEIGHT = C(i) \cdot DBH^2$, could not be located for white spruce and trembling aspen. As the exponent in this equation can range from 1.5 to 3.0 without drastically altering the shape of the final growth curve (Botkin et al. 1972b), an equation of the form $WEIGHT = C(i) \cdot DBH^{**}F$ was substituted. Accurate leaf biomass equations based on DBH were obtained (see below), and leaf weights were generated over a wide diameter range. Values of C and F that most closely duplicated these weights were determined using non-linear regression. Slight alterations to F values were required in fine tuning of the model.

As leaf biomass equations for white spruce and trembling aspen in the western Canadian boreal forest were not readily available, it was necessary to consider equations from other locations. This is justifiable because the birth and growth functions of JABOWA require relative and not absolute values of leaf weight. Singh (1982) contains suitable equations for predicting above-ground total-tree biomass without foliage for white spruce and trembling aspen in the prairie provinces. References containing equations for prediction of biomass per tree component were obtained. Leaf biomass equations were selected from the set of equations that

produced closest duplication of the above-ground total-tree minus foliage predictions of Singh (1982). The equations used were from those of Freedman et al. (1982), for white spruce and trembling aspen in Nova Scotia, and are given in Appendix III.

The inclusion of the exponential factor F required slight alteration of the growth rate equation. As mentioned, Botkin et al. (1972a,b) based their growth rate equation on the assumption that the change in volume of a tree is dependent upon, among other things, leaf area of the tree. They also assumed that leaf weight is proportional to leaf area. Consequently, tree growth is dependent upon leaf weight. Since JABOR does not consistently set a value of 2.0 for the exponent in the equation used for calculating leaf weight, as does JABOWA, the growth rate equation was changed from

$DINC = G \times DBH \times \dots$ (As shown on page 32)

to

$DINC = G \times DBH^{(F-1)} \times \dots$

4. Relationships between photosynthesis and available light:

a. Data for shade tolerance (ITYPE) were obtained from the literature. In the boreal forest, white spruce tends to be a tolerant species (Sutton 1969; Larsen 1980), while trembling aspen tends to be intolerant (Bella and DeFrancheschi 1980; Larsen 1980).

b. The value of the constant used in calculating shading leaf area, k , was altered. Botkin et al. (1972a) stated that the value of the constant was adjusted to obtain reasonable

shading beneath a dense canopy, and used a value of $1/6000$. In the preliminary runs of the JABOR model and in the validation data, the densest canopies had leaf weights of approximately 175.0 kg. Using k equal to $1/6000$ for such stands gives an available light level of 2.15×10^{-13} per cent of full light. To remedy this, the value of k was increased, and after fine tuning, a final value of $1/95000$ was used. This gives available light of about 15 per cent beneath a dense canopy, which was considered a reasonable approximation.

IV. BIOMASS EQUATIONS

As complete sets of reliable equations for calculation of biomass per tree component were not available for white spruce and trembling aspen in the western Canadian boreal forest, it was decided to limit JABOR to prediction of total-tree biomass. The equations of Singh (1982) were selected for calculation of above-ground, total-tree biomass without foliage. To obtain total aboveground biomass, leaf biomass was calculated using the leaf weight equations described earlier. The usage of equations derived outside the western Canadian boreal forest is justifiable in that the biomass equations used in JABOWA are very general, and the same sets of equations are used for up to five species. Also, the objective of this portion of the study was to produce a general trend of living biomass accumulation and not calculation of precise values.

The form of the equations of Singh (1982) does not allow them to be used below a DBH of 4.021 cm for white spruce and 5.028 cm for trembling aspen. To fill in these gaps, it was again necessary to use equations from outside the western Canadian boreal forest. For each species, the equation chosen gave the best transition to the above-ground total-tree prediction curves produced by the Singh (1982)-leaf weight combination. The criteria used were the comparative slopes of the prediction curves of the Singh (1982)-leaf weight combination and the equation being considered, and smoothness of the transition between them. Transition was made at the point, to the nearest one-thousandth of a centimeter, of smoothest transition. For both white spruce and trembling aspen, the anomaly was too small to significantly affect the results. The equations selected were from those of Baskerville (1965), for white spruce in Ontario, and Peterson et al. (1970) for trembling aspen near Calgary, Alberta.

All biomass equations used are included in Appendix III.

While searching through the literature, it was discovered that reliable and accurate root biomass equations were not available, and that there is a shortage of data on root-shoot ratios for tree species in the western Canadian boreal forest. Therefore, calculations of root biomass were not included in the model.

E. Collection of Validation Data

Validation data were obtained from three sources, as outlined below.

1. Alberta Forest Service permanent sample plot data were made available through Mr. Robert Morton, a doctoral student in the Department of Forest Science, University of Alberta. Permission to use the data was obtained from the Alberta Forest Service. The data were from over 200 groups of plots established in locations throughout Alberta. Each plot group consists of four plots, with most plots one-fifth or one-quarter acre in size. The plots range in initial age from 40 to 190 years, with the majority falling in the 75 to 125 year age range. Considerable gaps exist below 50 years and above 165 years. Each plot has from zero to three remeasurements, with most having one. The maximum period between initial and final measurements is 22 years, with most being on the order of 10 to 15 years. For each tree on a plot, species, DBH, an estimate of height, and crown class are recorded. Ages and diameter increments of selected trees are also included.

At the time of validation data collection, only white birch and jack pine had been eliminated from the model. Plot groups dominated by the remaining four species, or any combination thereof, were selected by stand age and type description. Selections were made to obtain the best possible representation of all age classes available, by

five-year intervals. When an age class could not be adequately represented by data from an initial plot measurement, plots with the appropriate age at remeasurement were chosen. A total of 44 plot groups was chosen, and these produced 57 groups of remeasurement plots. This resulted in a total of 404 individual plots.

2. Permanent sample plot data belonging to Proctor and Gamble Cellulose, Ltd., of Grande Prairie, Alberta, were also made available through Mr. Morton, and are from 20 plots established in the Grande Prairie area. Permission to use the data was obtained from Proctor and Gamble Cellulose, Ltd. All plots have been remeasured once, generally between five and ten years after plot establishment, giving a total of 40 sets of data. Initial stand ages range from 30 years to 75 years, with the majority in the 50 to 70 year range. All plots are 0.08 ha in size. Species, DBH, height estimate, crown class, and tree condition are recorded for each tree.

3. Temporary plot data were made available through Mr. Morton's doctoral research. A total of 23 plots were established on upland sites in the Alberta boreal forest. Age range was from 30 to 75 years, with the majority of stands 55 years and younger. Plot size ranged from 0.1 to 0.3 ha. For each tree, species, DBH, height estimate, stump diameter, and crown class were recorded. Where possible, tree age, and diameter increment for years 0 to 10, 11 to 20, and 21 to 30 were recorded.

All plots were analysed to generate data pertinent to validation of the JABOR model. Based on a plot size of 0.01 ha, the following data were obtained for each species present on a plot:

1. Frequency
2. Diameter distribution, based on the following diameter classes: 0-2.49 cm, 2.5-4.9 cm, 5.0-9.9 cm, 10.0-19.9 cm, 20.0-29.0 cm, 30.0-39.9 cm, 40.0-49.9 cm, 50.0-59.9 cm, 60.0-69.9 cm, 70.0-79.9 cm, 80.0-89.9 cm, 90.0 cm or greater
3. Average DBH
4. Maximum and minimum DBH
5. Average height

Total trees and total basal area were also calculated for the plot.

When balsam poplar and balsam fir were eliminated from the model, all plots that were judged to contain excessively high frequencies of these species were rejected. For the remaining plots, any coniferous species (including larch) present as minor constituents were incorporated into the data for white spruce, and minor deciduous components were assimilated into trembling aspen data.

After elimination of all unsuitable plots, a total of 227 plots remained. These included 195 Alberta Forest Service plots, 18 Proctor and Gamble plots, and 14 temporary plots. Distribution of plots by age class is shown in Table 4.

Table 4. Distribution of validation data plots by age class.

AGE CLASS (yr)	AFS	P&G	T-plot	TOTAL
30	0	2	2	4
35	0	3	3	6
40	3	3	3	9
45	0	0	1	1
50	0	0	0	0
55	7	3	3	13
60	10	2	0	12
65	7	1	1	9
70	5	1	0	6
75	11	1	1	13
80	6	0	0	6
85	23	0	0	23
90	7	0	0	7
95	16	1	0	17
100	10	1	0	11
105	8	0	0	8
110	8	0	0	8
115	20	0	0	20
120	8	0	0	8
125	8	0	0	8
130	8	0	0	8
135	3	0	0	3
140	6	0	0	6
145	0	0	0	0
150	10	0	0	10
155	0	0	0	0
160	1	0	0	1
165	3	0	0	3
170	0	0	0	0
175	7	0	0	7

AFS: Alberta Forest Service permanent sample plots

P&G: Proctor and Gamble Cellulose Ltd. permanent sample plots

T-plot: temporary sample plots belonging to Mr. R. Morton

For each age class, species averages of total trees per plot, number of trees per diameter class, and basal area were obtained.

F. VALIDATION PROCEDURES AND OBTAINING OF RESULTS

The basic purposes of model validation are to increase confidence in the predictive capabilities of the model (Shaeffer 1980), and to increase the ability of the model to simulate the real system it is intended to represent (Goodall 1972). Therefore, model validation is a subjective process that depends on who is using the model, and for what purposes (Holdaway and Brand 1981; Buchman and Shifley 1983). This is especially the case for models dealing with forest succession, as the phenomena that such models predict may span extensive time periods. Therefore, validation of these models usually relies upon inference rather than direct observation (Shugart and West 1980).

Considering the nature and scope of the present project, general and somewhat subjective procedures were deemed to be adequate for validating the results of JABOR (K.O. Higginbotham, B. L. Phillips, S. J. Titus, personal communications). The basic procedure used was to adjust program parameters and functions until 25 stochastic runs of the model produced averages of species basal areas, frequencies, and diameter distributions that gave reasonable fits to the averages of the validation data.⁸ As the

⁸It was decided that averages obtained from 25 stochastic runs would permit adequate validation of the model results

validation data are a composite of different stands, with varying site indices, stand densities, and number of plots available per age class, they are not a true representation of the phenomena and processes that occur during a real-life successional sequence. As a result, the observed stands often show irregularities and fluctuations in trends of species basal areas, frequencies, and diameter distributions. Consequently, model results that were deemed to best follow the general trends exhibited by the validation data were obtained.

Statistical analyses and comparisons of validation data and model results were not attempted, because although statistical tests are useful guides, statistically significant prediction errors are not necessarily significant in the practical sense (Goodall 1972). Also, Buchman and Shifley (1983) stated that statistical tests can rarely be used to accept or reject the hypothesis that a growth model is a useful representation of a natural system.

As no validation data were available for stands less than 30 years of age, the predictions of the model for this age range must be treated with caution, and are not included in this report. Although validation data were not available for stands older than 175 years, model predictions for ages up to 200 years were obtained. It was felt that simulation of stand dynamics of older stands is more accurate than

^a(cont'd) (K. D. Higginbotham, B. L. Phillips, personal communications). Age class interval was five years; duration of simulation runs is discussed shortly.

simulations for stands younger than 30 years, and more confidence can be expressed in the predictions for the older stands.

As analytical forest growth models are useful for extrapolative purposes, the first ten stochastic runs were extended to a length of 500 years, at 10-year age class intervals. However, the relationships and functions of JABOR may not be accurate representations of the ecological processes and mechanisms that occur in stands up to 500 years of age, and any conclusions drawn from these long-term predictions are purely speculative.

V. RESULTS AND DISCUSSION

In this section, model predictions for stands between 30 and 200 years of age are averages of 25 stochastic runs, and predictions for stands between 210 and 500 years of age are averages of 10 stochastic runs. The validation data values are the averages of all plots available in an age class. Validation data for trembling aspen at year 45 were deleted, as the one plot available at this age class showed a very high comparative density of aspen. Validation data for white spruce at year 160 were also deleted, as the one available plot had a very low comparative density of spruce. All figures in this section are shown in tabular form in Appendix IV.

A. TREMBLING ASPEN

Basal Area

Figure 4 shows JABOR predictions for basal area of trembling aspen, for years 30 to 200, compared to values derived from the validation data.

Observed basal area values for trembling aspen show rather wide and abrupt fluctuations, since the validation data represent a composite of different stands, and not temporal development of one or more stands. Despite this, predicted basal areas show a generally good fit to the observed values, occupying a middle position through the

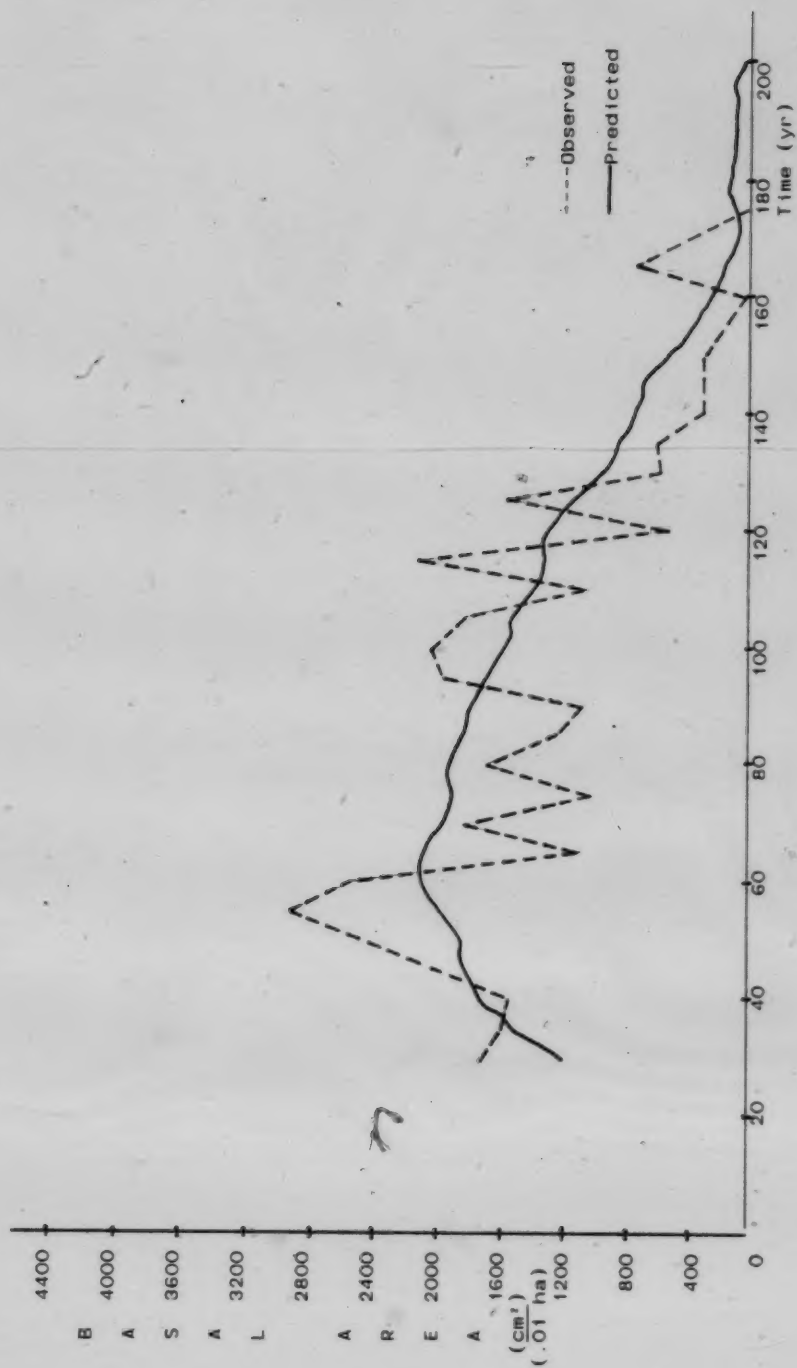


Figure 4. Comparison of JABOR predictions of average basal area by age class for trembling aspen to average basal area values of the validation data.

fluctuations of the validation data. One exception is at year 165, where all three validation plots were from the same Alberta Forest Service permanent sample plot group, and contained comparatively high numbers of aspen in the 40.0-49.999 cm diameter class.⁹

It can be seen that the simulated peak basal area (2075 cm²) is somewhat lower than the observed maximum (2534 cm²). This is a difference of only 18%, and may be due to inherent variability within the validation data. The fact that peak basal area for trembling aspen occurs at year 60 for the validation data and year 65 for the model predictions is insignificant, as the predicted or observed peak could shift according to the number of runs or plots used.

Predicted basal area for trembling aspen after year 150 would have corresponded much more closely to observed values, except for the effects of one particular simulation run. In this run, white spruce showed relatively poor establishment, and periods of relatively high mortality. Consequently, four large trembling aspen trees were able to survive, and produced basal areas of up to 2665 cm². In comparison to other runs, and to the available validation data, such basal area values are exceptionally high.

Even if the run just described was eliminated, predicted basal area between years 130 and 160 would be somewhat high. If validation data were available for years 145 and 155, and more data were available for several other

⁹The fourth plot of this group had been eliminated, due to an excessively high frequency of white birch.

age classes, observed basal area in these years may have been closer to predicted values. If predicted basal area was decreased by altering the birth and/or mortality functions, or the species-specific growth rate constant, underestimation in earlier years resulted. As well, species frequencies and/or diameter distributions were often adversely affected.

In general, any predicted basal area for trembling aspen from years 135 to 180 results from one tree in the 20 to 45 cm diameter range being present on one or more runs. The basal areas of these runs are then averaged in with runs with no aspen present, or very small aspen basal areas. As stand age increases, the probability of the one large trembling aspen tree surviving decreases, and this causes average basal area for aspen to steadily decrease with time.

There are exceptions to this norm, however. In a number of cases, a pure white spruce stand will open up, due to the almost simultaneous deaths of the largest trees, or a rather large number of trees. This reduces plot shading, which increases the chances of trembling aspen establishing from a parent tree or seed source outside the plot, and decreases the chance that saplings which do establish will die from suppression. As a result, there are instances where one or two small aspen trees are present on a plot, and constitute basal areas of 25 cm² or less. In nearly all cases where trembling aspen establishes by this mechanism, most trees are relatively short-lived, as the remaining white spruce

trees sooner or later effect canopy closure, and cause mortality of the aspen by suppression.

Between years 180 and 200, a large proportion of predicted basal area for trembling aspen is contributed by the one run in which basal area reaches comparatively high values. The remainder is generally derived from aspen ingrowth contributing 10 cm² or less of basal area.

Figure 5 shows predicted basal area of trembling aspen up to year 500, with predicted values for years 30 to 200 included for ease of comparison. The long-term runs do not include the one run which produced exceptionally high basal area for trembling aspen. After year 200, all age classes show at least some basal area present, with the amount present depending mainly upon the extent of shading by white spruce. This is illustrated by the increase, and subsequent decrease, in basal area of trembling aspen between years 360 and 430, which corresponds to a period in which a number of plots exhibited rather extensive opening and subsequent closure of pure or almost pure white spruce stands. As well, all plots showed from one to three cycles in which trembling aspen established in response to varying degrees of stand opening, and then eventually disappeared.

In general, the long-term basal area predictions would seem to be rather high, as all except one of the ten runs showed maximum values of over 100 cm². Two runs showed maxima of over 500 cm², although one of these runs produced this maximum with trees established prior to year 200. Any

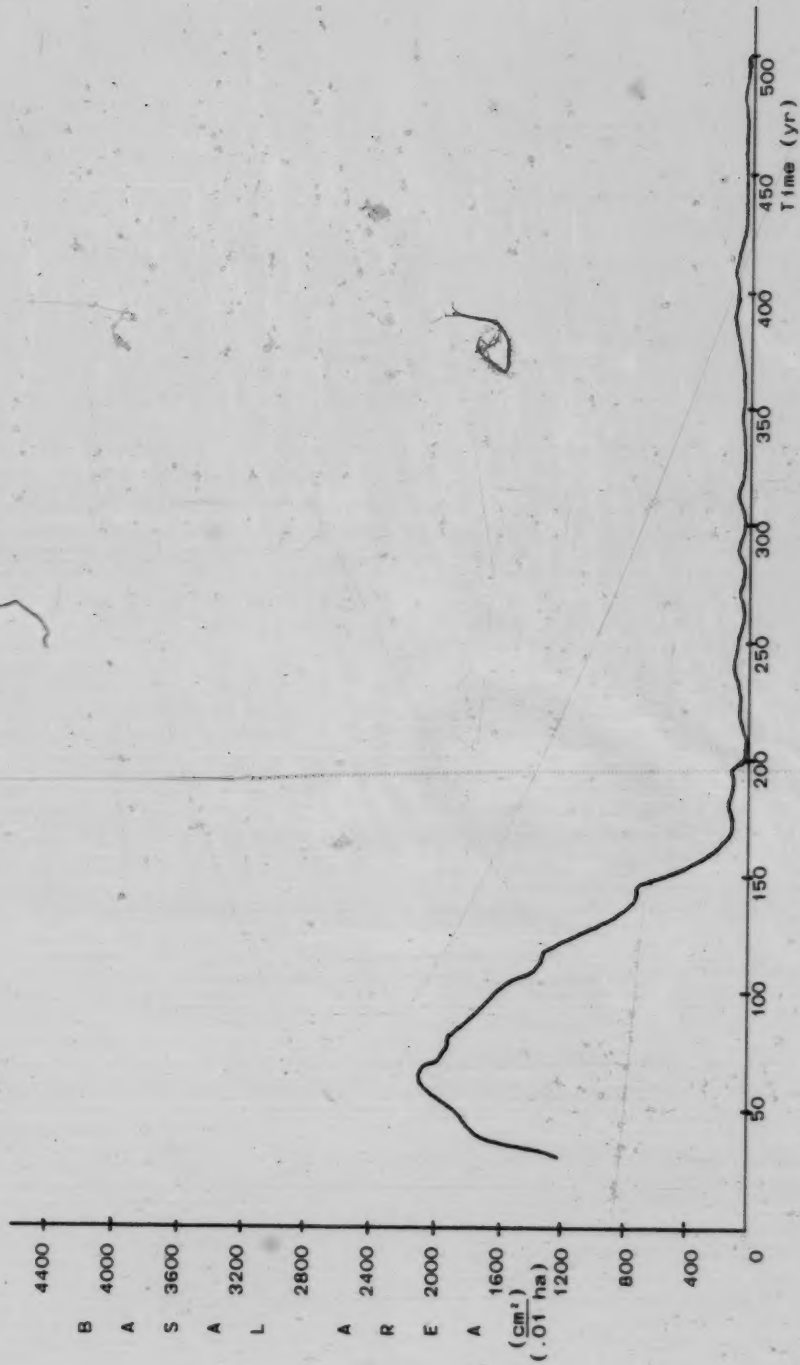


Figure 5. Predictions of average basal area by age class for trembling aspen between 30 and 500 years.

overestimation probably results from the birth function of JABOR not fully accounting for possible reductions in numbers of parent trees available as sprout or seed sources. In nature, it is probable that as the larger, potentially most-reproductive trembling aspen trees die, they will not be replaced, and the available reproductive stock will be increasingly reduced. In the model, the lowest probability level for introduction of trembling aspen ensures close simulation of observed basal area values up to year 175. However, it appears that this probability level is sufficiently high to maintain these basal area values to year 500 for the majority of the runs.

Frequency

Figure 6 shows predicted versus observed frequency values for trembling aspen.

Predicted frequencies of trembling aspen show a good fit to the observed values, especially from year 100 onwards. Between years 30 and 50, and years 65 and 95, predicted frequencies are somewhat higher than observed values. However, these periods correspond to periods in which predicted basal area exceeds observed basal area.

Figure 7 shows the long-term predictions for trembling aspen frequency. As was the case with basal area, frequency of trembling aspen shows cycles of increase and decrease. There would appear to be overestimation of long-term frequencies, and this would again be the result of the

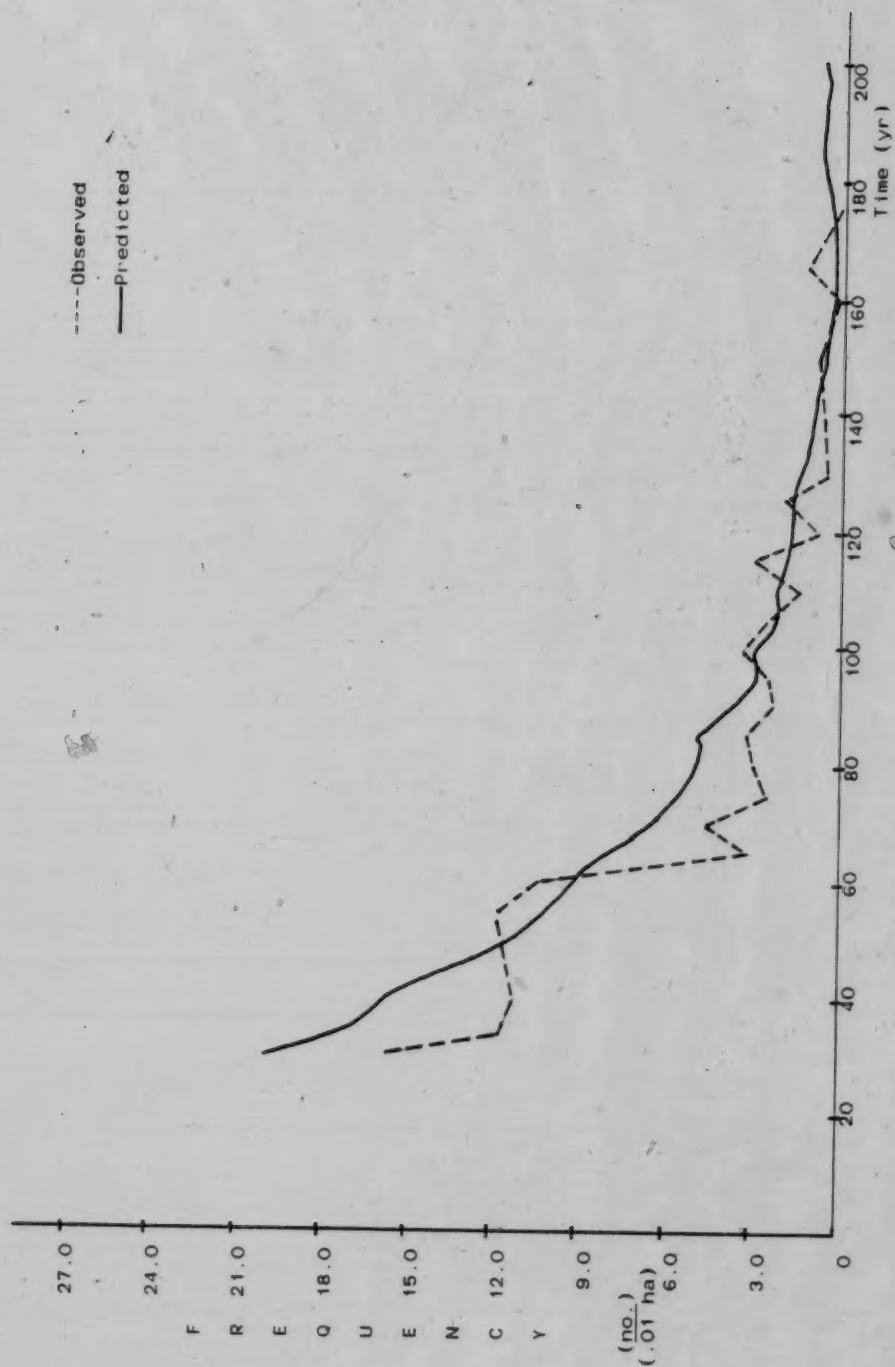


Figure 6. Comparison of JABOR predictions of average frequency by age class for trembling aspen to average frequencies of the validation data.

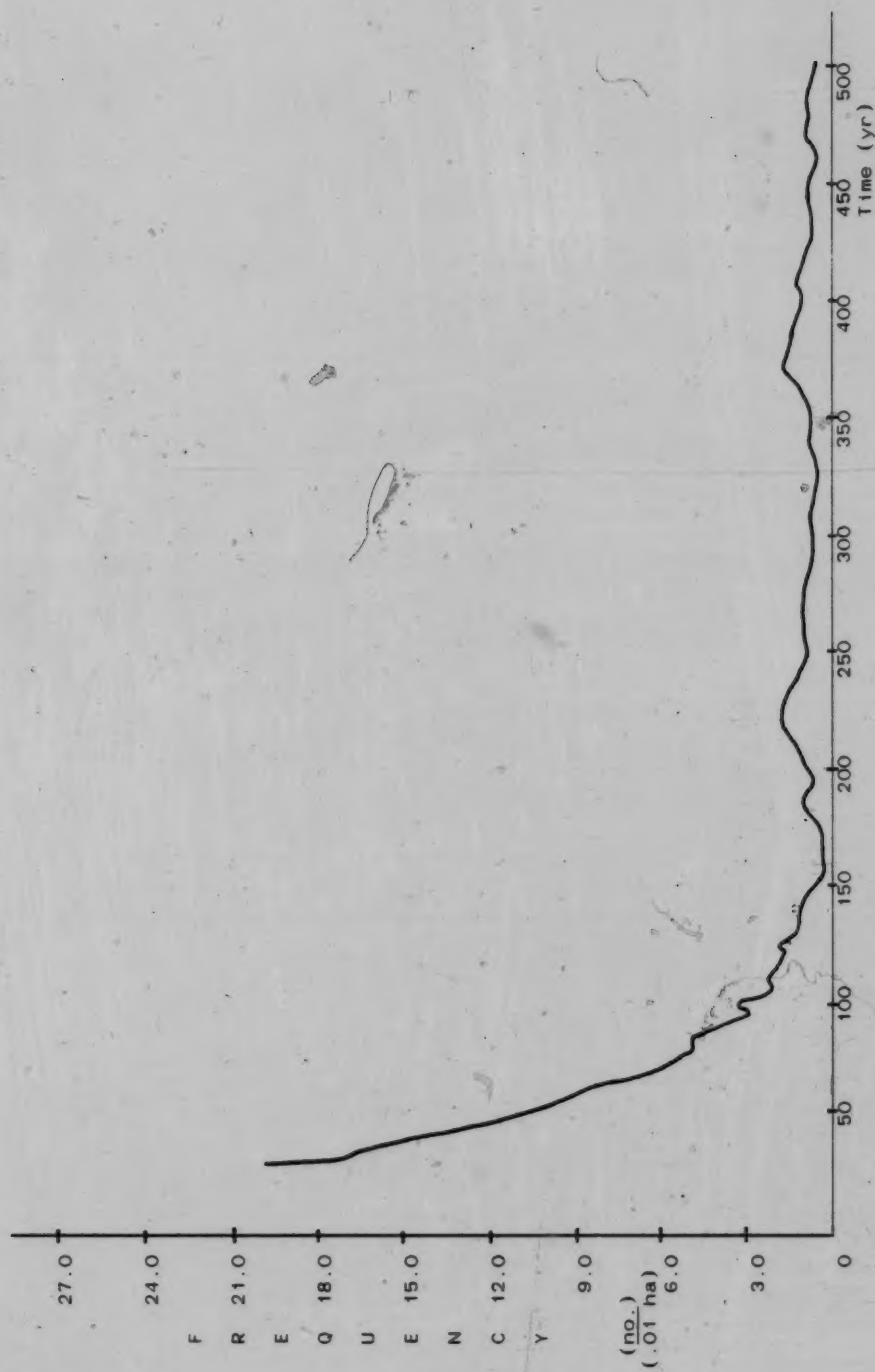


Figure 7. Predictions of average frequency by age class for trembling aspen between 30 and 500 years.

nature of the birth function for trembling aspen. While four runs showed establishment of five or less trees after year 200, five runs showed establishment of nine or more trees in this period.

Individual model runs show wide variability in the stand age at which trembling aspen initially disappears from the simulated plots.¹⁰ The earliest stand age at which no aspen are present is 95 years, and except for the one run in which large-sized trembling aspen remain until year 200, the latest age of disappearance is 180 years. On 18 of the 24 runs in which aspen is eliminated, the last tree(s) to disappear date back to within 30 years of stand origin. On the remaining five runs, the last trembling aspen tree(s) date(s) from approximately 30 to 50 years after stand origin. The run in which aspen is eliminated by year 180 is an exceptional case. A trembling aspen sapling established shortly before the largest aspen, which dated to 35 years after stand origin, died, and another sapling established immediately after the death. The oldest sapling soon died, but the youngest one persisted for 15 more years. For the 24 runs, the average stand age of disappearance is 134.2 years. This is a reasonable age, because up to and including year 165, the validation data consistently show trees in the 40.0-49.9 cm diameter class. These trees could date back to, or near, stand origin.

¹⁰This discussion does not include those instances where one or more trembling aspen saplings establish after the species has initially disappeared from the stand, and persist for a short period of time.

Diameter Distribution

Table 5 shows predicted versus observed diameter distributions for trembling aspen.

The validation data often show wide variation between consecutive age classes within diameter classes. Despite this, there is generally good agreement between predicted and observed distributions, as most predicted tree numbers are within 0.6 or 0.7 trees of observed values. There are a few isolated cases where there is under or over-prediction of between 1.0 and 1.9 trees. Cases where differences are greater than 2.0 trees tend to be clumped, and occur in the middle diameter classes, as follows:

1. 5.0-9.999 cm: over-prediction at year 30;
under-prediction in years 35 to 55.
2. 10.0-19.999 cm: over-prediction in years 35 and 40.
3. 20.0-29.999 cm: under-prediction in years 65 to 85.¹¹

It can be seen that for the 10.0-19.999 cm and 20.0-29.999 cm diameter classes, differences between predicted and observed diameter distributions correspond directly to areas where observed basal area and frequency fluctuate around predicted basal area and frequency. Except for year 40, this is also the case for the 5.0-9.999 cm class.

In some cases, the validation data show no trees in the 0-2.499 cm diameter class, while the model predicts 0.04 to 0.2 trees. Such overestimations may not in fact be real, as

¹¹Year 85 shows a difference of 1.5 tree. This is the only instance where a difference of between 1.0 and 1.9 trees does not occur as an isolated case.

Table 5. Comparison of JABOR predictions of average diameter distribution per age class of trembling aspen to average diameter distribution of the validation data (no. trees/0.01 ha).

Age Class (yr.)	DIAMETER CLASS (DBH in cm)															
	0-2.499	2.5-4.999	5.0-9.999	10.0-19.999	20.0-29.999	30.0-39.999	40.0-49.999	50.0-59.999	60.0-69.999	70.0-79.999	80.0-89.999	90.0-99.999	100.0-109.999	110.0-119.999	120.0-129.999	130.0-139.999
30	1.10/0	0.80/0	12.00/8.70	5.90/6.80	0	0	0	0	0	0	0	0	0	0	0	0
35	1.00/0.30	1.00/0.70	3.20/5.70	11.80/3.90	0	0	0	0	0	0	0	0	0	0	0	0
40	1.40/0.60	0.80/0.40	1.10/3.90	12.40/5.60	0	0	0	0	0	0	0	0	0	0	0	0
45	1.10/0	1.10/0.80	0.90/9.20	10.20/10.8	0	0	0	0	0	0	0	0	0	0	0	0
50	0.70/0	1.10/0	1.00/0	8.70/0	0	0	0	0	0	0	0	0	0	0	0	0
55	0.70/0.20	0.60/0.10	1.10/3.20	6.80/6.10	1.00/1.90	0	0	0	0	0	0	0	0	0	0	0
60	0.60/0.30	0.50/0.50	1.10/1.70	4.20/5.10	2.90/2.50	0	0	0	0	0	0	0	0	0	0	0
65	0.40/0.04	0.40/0.30	1.10/0.40	1.90/0.90	4.10/1.10	0	0	0	0	0	0	0	0	0	0	0
70	0.04/0	0.40/0	0.90/0.40	1.10/2.30	4.00/0.90	0	0	0	0	0	0	0	0	0	0	0
75	0	0.40/0.02	0.70/0.20	0.90/1.20	3.80/1.10	0	0	0	0	0	0	0	0	0	0	0
80	0.02/0	0.30/0.05	0.50/0.40	1.00/0.70	3.30/0.80	0	0	0	0	0	0	0	0	0	0	0
85	0.10/0	0.20/0	0.40/0.10	0.90/1.70	2.70/1.20	0	0	0	0	0	0	0	0	0	0	0
90	0.04/0.03	0.20/0.04	0.40/0.10	0.70/0.60	2.00/1.20	0	0	0	0	0	0	0	0	0	0	0
95	0.04/0.02	0	0.20/0.10	0.40/0.30	1.20/1.10	0	0	0	0	0	0	0	0	0	0	0
100	0.04/0	0	0.40/0.06	0.60/0.80	0.80/1.50	0	0	0	0	0	0	0	0	0	0	0
105	0	0	0.20/0.03	0.40/0.20	0.40/0.10	0	0	0	0	0	0	0	0	0	0	0
110	0.20/0.01	0	0.04/0	0.40/0.10	0.40/0.70	0	0	0	0	0	0	0	0	0	0	0
115	0.10/0	0.04/0.30	0	0.40/0.40	0.30/0.90	0	0	0	0	0	0	0	0	0	0	0
120	0.10/0	0.08/0.04	0	0.10/0.20	0.40/0.10	0	0	0	0	0	0	0	0	0	0	0
125	0.10/0	0.20/0	0.04/0.10	0.08/0.09	0.30/0.60	0	0	0	0	0	0	0	0	0	0	0
130	0.10/0.03	0.20/0.10	0.04/0.01	0.08/0.06	0.20/0.01	0	0	0	0	0	0	0	0	0	0	0
135	0.04/0	0.10/0	0.20/0	0.04/0.10	0.10/0.10	0	0	0	0	0	0	0	0	0	0	0
140	0.08/0.08	0.08/0.08	0.08/0.10	0.04/0.10	0.10/0.10	0	0	0	0	0	0	0	0	0	0	0
145	0.04/0	0.10/0	0.08/0	0.04/0	0.10/0	0	0	0	0	0	0	0	0	0	0	0
150	0.10/0.10	0.04/0.20	0.08/0.08	0	0	0	0	0	0	0	0	0	0	0	0	0
155	0.04/0	0	0	0.08/0.08	0.10/0.05	0	0	0	0	0	0	0	0	0	0	0
160	0	0	0	0.08/0.20	0.10/0	0	0	0	0	0	0	0	0	0	0	0
165	0.04/0	0	0	0.08/0.10	0.10/0.10	0	0	0	0	0	0	0	0	0	0	0
170	0.10/0	0	0	0.08/0.08	0.10/0.08	0	0	0	0	0	0	0	0	0	0	0
175	0.20/0	0.04/0.08	0	0.04/0.01	0.04/0	0	0	0	0	0	0	0	0	0	0	0
180	0.30/0	0.10/0	0.04/0	0.04/0	0.04/0	0	0	0	0	0	0	0	0	0	0	0
185	0.30/0	0.20/0	0.10/0	0.04/0	0	0	0	0	0	0	0	0	0	0	0	0
190	0.30/0	0.30/0	0.10/0	0.04/0	0	0	0	0	0	0	0	0	0	0	0	0
195	0.30/0	0.10/0	0.10/0	0.04/0	0	0	0	0	0	0	0	0	0	0	0	0
200	0.30/0	0.20/0	0.20/0	0.04/0	0.04/0	0	0	0	0	0	0	0	0	0	0	0

P=Predicted
O=Observed

*The validation data showed 0.03 trees with DBH greater than 70.0 cm at year 170. No model runs recorded trees of this size.

the tendency when doing volume or merchantability-oriented field measurements is to pay more attention to larger trees, and to ignore and not record trees of smaller diameters. This is in fact the case for the majority of the Alberta Forest Service permanent sample plots (R. Morton, personal communication). It would also seem probable that small trees of the less commercially-used species, such as trembling aspen, would be ignored more often. Therefore, the model may overestimate recorded numbers, but not necessarily actual numbers.

It can be seen that all diameter classes larger than the 2.5-4.999 cm class exhibit a general pattern in which observed and actual numbers of trees reach a respective maximum, and then show an overall decline with time. Although the actual points at which the maxima occur are difficult to discern, it is possible to obtain reasonable approximations.

Between years 175 and 200, there are no prominent changes in predicted diameter distributions of trembling aspen. In general, those diameter classes larger than the 5.0-9.999 cm class continue to exhibit decreases in numbers of trees, with the 30.0-39.999 cm and 40.0-49.999 cm classes showing complete disappearance of aspen. The very slight increase in number of trees in the 0-2.499 cm diameter class, which began in year 170, is continued, as a number of runs show extensive opening of overmature stands. The effects of stand opening reach the 2.5-4.999 cm diameter

class by year 175, but in a reduced proportion to the 0-2.499 cm class. The effect on the 5.0-9.999 cm class is even slighter, and is visible by year 185. There is no effect on any of the larger diameter classes, as all ingrowth suffered suppression mortality, due to stand closure, before reaching a diameter of 10.0 cm. All trees recorded in the 10.0-19.999 cm and 20.0-29.999 cm classes were from the one run which produced comparatively high basal areas of trembling aspen.

In a number of age classes, the JABOR predictions could not match observed number of trees in the larger diameter classes without seriously biasing the results. In such cases, duplication of the observed stands would require using a growth rate constant for trembling aspen that is much higher than the one used in the model. This would increase the rate at which trees grow out of the smaller diameter classes and into the larger ones, and cause serious distortion of predicted diameter distributions and basal areas for trembling aspen.

Much of this problem is a result of wide variability in stand histories of the observed plots. While it can be assumed that all or most of these stands were originated by fire, fires can vary widely as to type, severity, areal extent, and effects upon vegetation and habitat (Kelsall et al. 1977; Alexander and Euler 1981). Although trembling aspen is not a strongly fire-resistant species (Day and Harvey 1981), it would not be unreasonable to assume that at

least some of the trees in question are residuals that survived the fires that originated the stands. It is, however, impossible to determine exactly which trees are residuals, and their exact size at stand origin, and to input them into the beginning of the model runs, which begin with bare-ground conditions. Another possibility is that the large trees had better inherent growth potentials, due to variations in genetic characteristics, or in site characteristics. In JABOR, the growth rate constants are fixed for all trees of a species.

Holdaway and Brand (1981) and Buchman and Shifley (1983) stated that no growth model can perfectly represent the system being simulated, and most models are very much limited to reproduction of the average type of stand of the community or ecosystem they are designed to simulate. Therefore, it was decided to sacrifice inclusion of all observed diameter classes per age class for the overall accuracy of the model. In only five instances where this situation occurs do observed numbers of trees exceed 0.3, and in no cases were more than 0.9 trees present.

The problem just discussed also affected prediction of the largest-sized trees occurring in the simulation runs. For example, the validation data recorded one trembling aspen tree exceeding 70.0 cm DBH, and seven trees in the 60.0-69.999 cm diameter class. By comparison, the model produced no trees greater than 60.0 cm DBH, and one tree in the 50.0-59.999 cm class. It should be pointed out that the

values used in the model for DBHMAX, HTMAX, and AGEMX also imposed constraints upon the largest diameters attainable by trembling aspen, and the number of trees reaching these diameters.

The long-term predictions for diameter distributions of trembling aspen would reflect any overestimation within the predictions for frequency. For example, the 0-2.499 cm. and 10.0-19.999 cm diameter classes each show only one age class with no trees recorded. In general, numbers of trees in the 0-2.4999 cm, 2.5-4.999 cm, and 5.0-9.999 cm diameter classes remain relatively close to levels present before year 200. However, the 10.0-19.999 cm diameter class shows a slight increase, with tree numbers fluctuating between 0.1 and 0.3. Of trees that established after year 200, two exceeded 20.0 cm DBH.

Biomass

Figure 8 illustrates the predictions of JABOR for accumulation of above-ground, total-tree living biomass¹² of trembling aspen.

Trembling aspen biomass shows a rather steep rate of accumulation until year 65. Between years 65 and 90, there is very little change in biomass, with a maximum occurring at year 80. After year 90, there is a moderately steep overall decrease to year 200. Between years 200 and 500,

¹²Except where more specificity is required, the phrase "above-ground total-tree living biomass" is interchangeable with "living biomass" and "biomass".

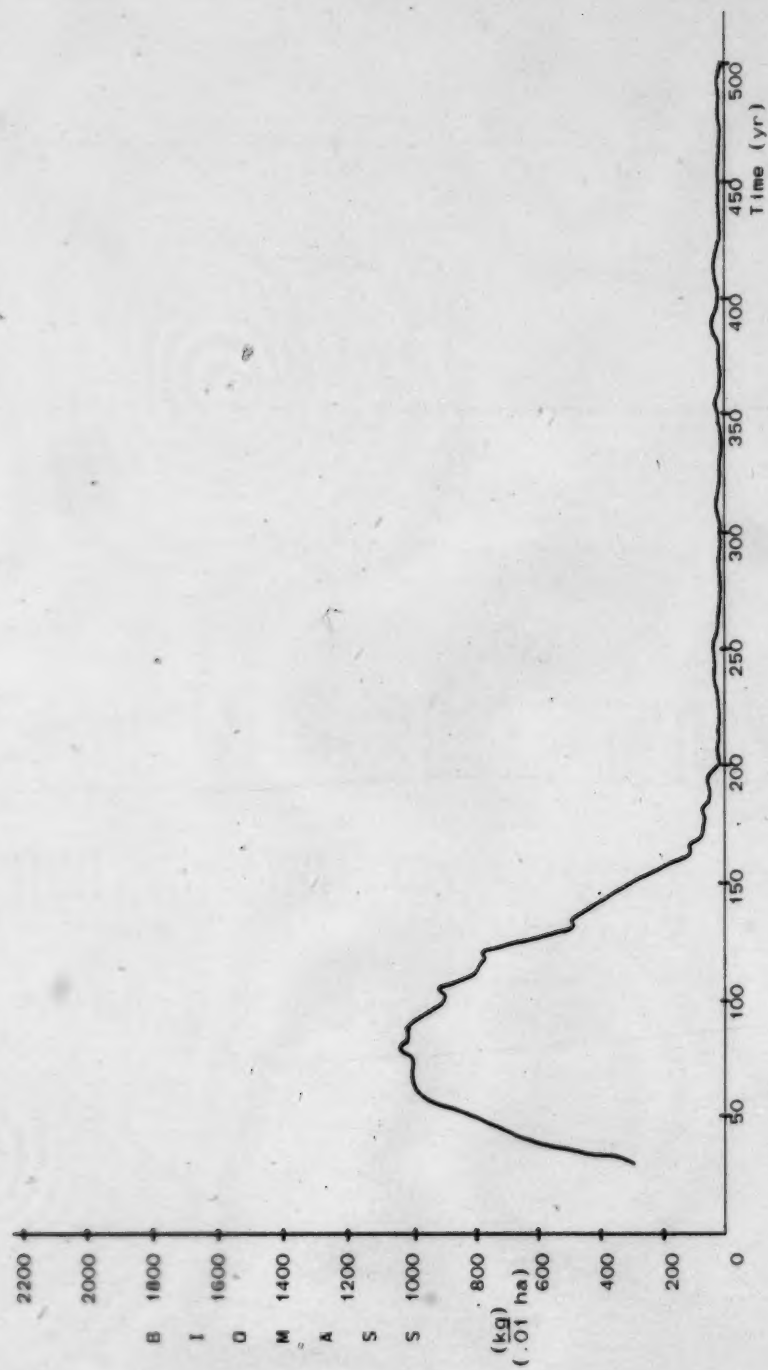


Figure 8. Predictions of average biomass by age class for trembling aspen between 30 and 500 years.

most biomass values are less than 20 kg, and the overall average is 16 kg. As expected, biomass of trembling aspen follows the same general pattern as basal area.

B. WHITE SPRUCE

Basal Area

Figure 9 is a representation of the model predictions for basal area of white spruce, compared to values obtained from the validation data.

Predicted basal area values show a generally good fit to the observed values. An exception is year 175, where all validation plots show either comparatively high white spruce frequencies, or comparatively large numbers of trees in the 30.0-39.999 cm diameter class. After year 150, it is difficult to determine a trend in observed basal area. Although there appears to be an overall decline characterized by erratic fluctuations, this may not necessarily be the case, especially if values are weighted by the number of plots available per age class. It can be seen, however, that the model predictions exhibit this pattern. If validation data were available for years 145, 155, and 170, and more data available for other age classes, a more definite trend of observed basal area for this time period could have been discerned.

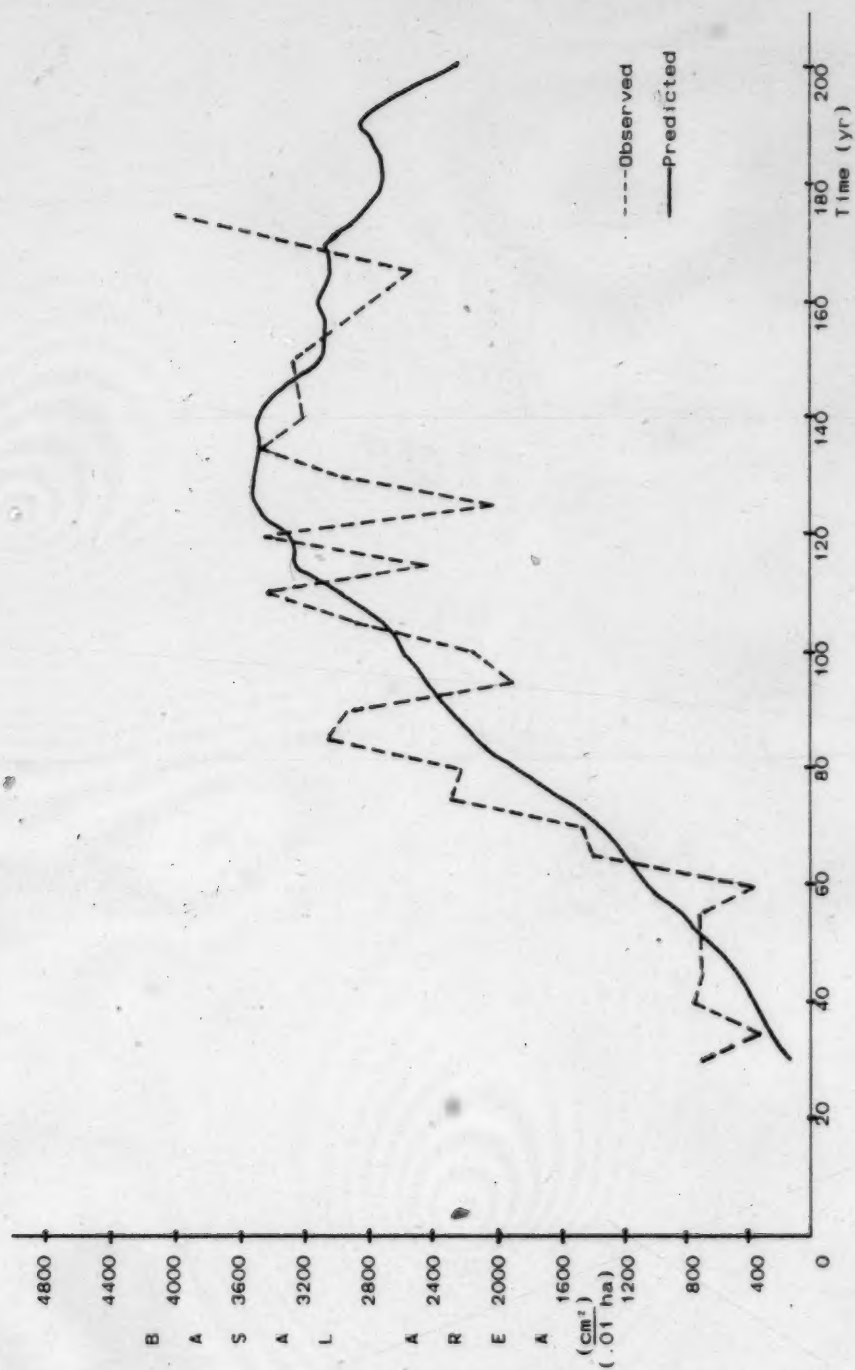


Figure 9. Comparison of JABOR predictions of average basal area by age class for white spruce to average basal area values of the validation data.

The fact that the model shows peak white spruce basal area at year 130, while the validation data show a peak at year 135, is insignificant. As was the case for trembling aspen, the observed or predicted peak for white spruce could be shifted according to the number of plots or runs used.

There are no particular model runs which have a prominent effect upon the shape or slope of the predicted basal area accumulation curve, or any portion of it. The predicted basal area curve is rather smooth, as it is the average of 25 model runs. However, small yearly random effects can produce wide variation between individual runs when viewed at a single point in time. Table 6 shows the variability of white spruce basal area at selected stand ages. No two of the minimum and maximum values given in Table 6 are from the same simulation run.

Table 6. Examples of stochastic variation in the predictions of JABOR for basal area of white spruce.

AGE CLASS (yr)	MINIMUM BASAL AREA (cm ² /.01 ha)	MAXIMUM BASAL AREA (cm ² /.01 ha)	AVERAGE BASAL AREA OF 25 MODEL RUNS (cm ² /.01 ha)
50	133	1404	673
80	422	3310	1900
110	1396	5006	2980
140	1021	7351	3500
165	1166	7199	3050
185	199	6488	2749

Table 6 illustrates how the stochastic nature of the model allows reproduction of the variability that occurs among

boreal mixedwood stands.

Figure 10 shows the long-term predictions of basal area for white spruce. White spruce exhibits cycles of oscillations of basal area, corresponding to periods in which individual overmature plots or patches undergo concurrent or almost concurrent break-down, and varying degrees of recovery. While the oscillations vary in magnitude, white spruce does not show any long-term losses in basal area.

Frequency

Figure 11 shows predicted versus observed frequency by age class of white spruce.

Within the validation data, variations of five or six trees between consecutive age classes are not uncommon. Predicted frequencies show relatively little fluctuation, and tend to be consistently higher than the observed values. This is due mainly to over-prediction in the 0-2.499 cm diameter class (see page 92).

The long-term predictions illustrated in Figure 12 show white spruce undergoing cycles of moderate fluctuation in frequency. Although three individual runs showed white spruce frequencies as low as three trees, no runs experienced break-down or deterioration sufficient to allow prolific invasion and establishment of trembling aspen. The low frequencies would suggest that deterioration could at times be rather extensive, and could produce exceedingly

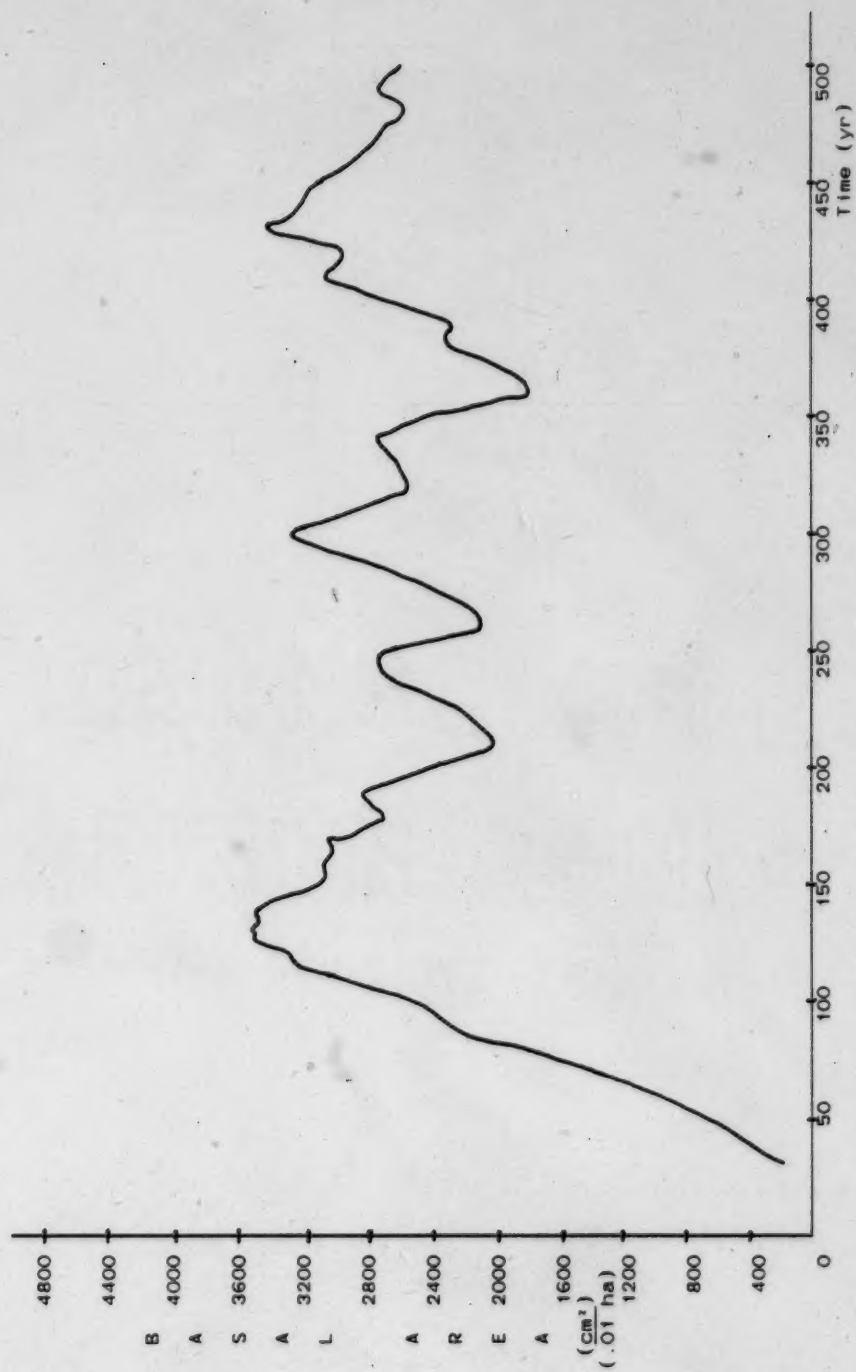


Figure 10. Predictions of average basal area by age class for white spruce between 30 and 500 years.

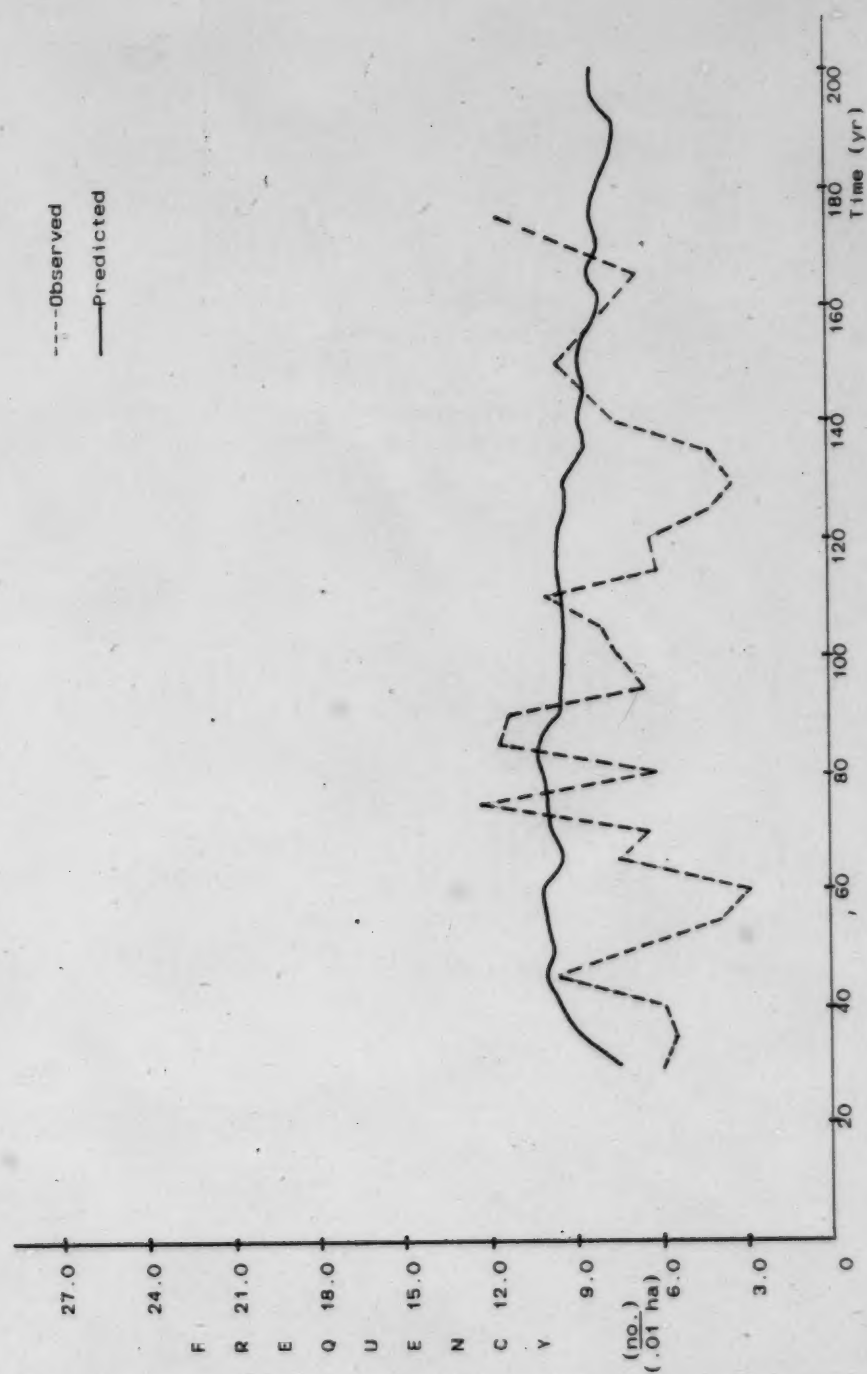


Figure 11. Comparison of JABOR predictions of average frequency by age class for white spruce to average frequencies of the validation data.

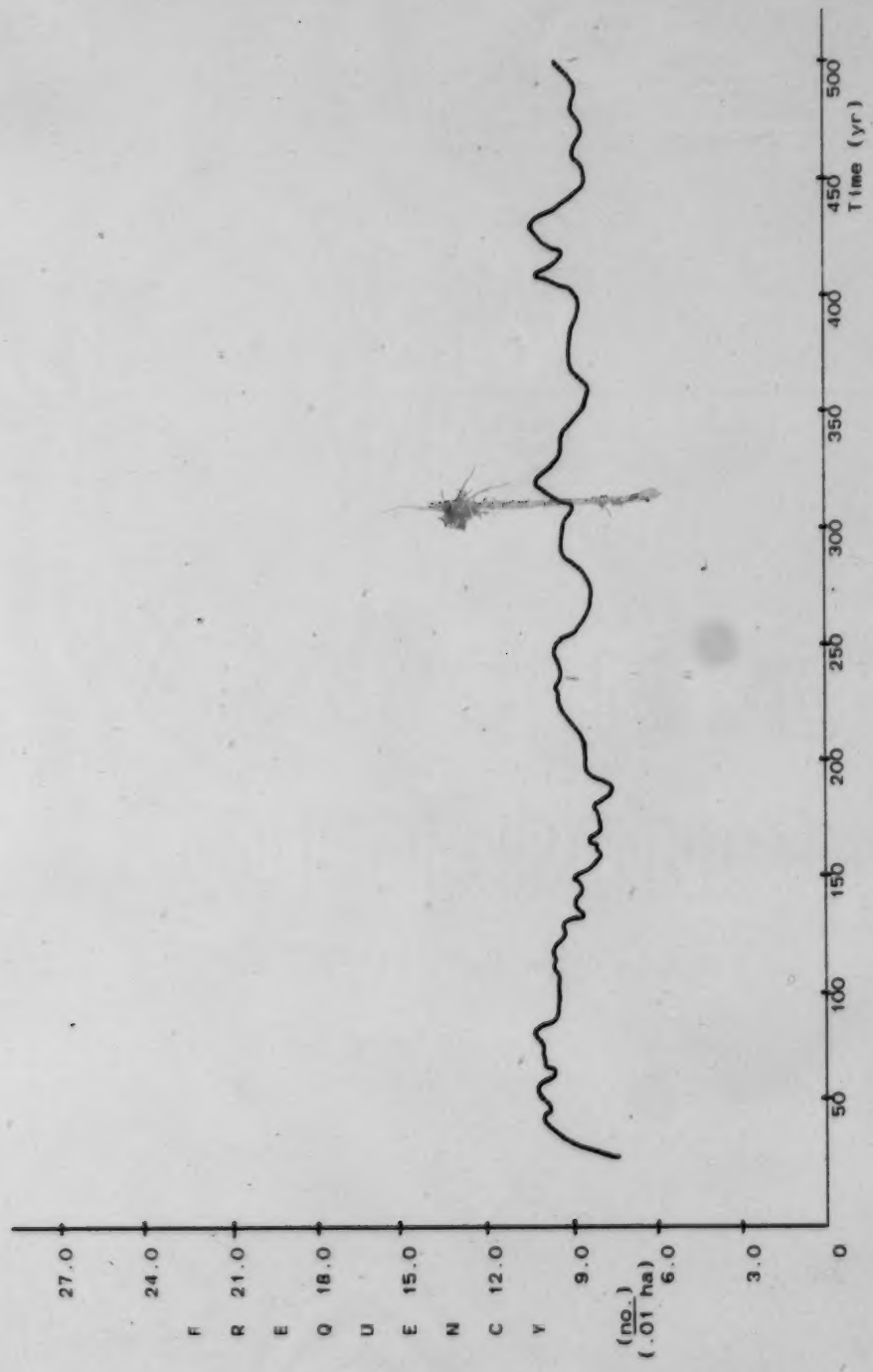


Figure 12. Predictions of average frequency by age class for white spruce between 30 and 500 years.

overmature or decadent plots or stands.

Diameter Distribution

Table 7 shows predicted versus observed diameter distributions of white spruce.

The validation data often show rather wide variation between consecutive age classes within diameter classes. Despite this, the predicted distributions show a generally good fit to the observed distributions. As was the case for trembling aspen, the model predictions often did not match the observed numbers of trees in the larger diameter classes. In only five cases where this occurred were observed numbers of trees greater than 0.1 trees, and in no cases were more than 0.9 trees present. It would again be reasonable to assume that at least some of the trees in question are residuals that survived fires that originated the stands. This conclusion is supported by the observations that white spruce is somewhat more fire-resistant than trembling aspen, and increases slightly in fire resistance as height increases and bark thickens (Day and Harvey 1981). It is also possible that some of the large white spruce trees possessed comparatively high inherent growth potentials.

The model consistently overestimates the number of trees in the 0-2.499 cm diameter class. There is also frequent overestimation in the 2.5-4.999 cm class. However, the magnitude of overestimation is less, as a large

Table 7. Comparison of JABOR predictions of average diameter distribution per age class of white spruce to average diameter distribution of the validation data (no. trees/0.01 ha).

Age Class (yr.)	DIAMETER CLASS (DBH in cm)															
	0-2.499	2.5-4.999	5.0-9.999	10.0-19.999	20.0-29.999	30.0-39.999	40.0-49.999	50.0-59.999	60.0-69.999	70.0-79.999	80.0-89.999	90.0-99.999	100.0-109.999	110.0-119.999	120.0-129.999	130.0-139.999
30	2.60/0	2.10/0.70	2.40/3.00	0.30/2.00	0	0	0	0	0	0	0	0	0	0	0	0
35	2.70/0.30	2.10/1.00	2.70/3.00	1.20/1.10	0	0	0	0	0	0	0	0	0	0	0	0
40	2.20/0.50	2.10/1.00	3.10/2.20	1.90/1.90	0	0	0	0	0	0	0	0	0	0	0	0
45	2.10/0.40	2.10/0.40	2.80/6.40	2.90/2.40	0	0	0	0	0	0	0	0	0	0	0	0
50	1.50/0	1.90/0.50	2.80/0.50	3.50/0.50	0	0	0	0	0	0	0	0	0	0	0	0
55	1.90/0.08	1.70/0.50	2.40/1.20	3.80/1.40	0.10/0.60	0	0	0	0	0	0	0	0	0	0	0
60	1.80/0.05	1.10/0.20	2.60/0.60	3.70/0.80	0.70/0.30	0	0	0	0	0	0	0	0	0	0	0
65	1.20/1.10	1.40/1.50	2.10/1.40	3.80/1.80	1.00/1.10	0	0	0	0	0	0	0	0	0	0	0
70	1.60/0.10	1.10/0.40	2.00/1.90	3.50/2.60	1.60/1.10	0	0	0	0	0	0	0	0	0	0	0
75	1.30/0.50	1.20/1.80	1.90/2.80	3.40/4.50	2.10/1.70	0	0	0	0	0	0	0	0	0	0	0
80	1.50/0	1.10/0.06	1.60/0.50	3.20/3.00	2.50/2.00	0.08/0.50	0	0	0	0	0	0	0	0	0	0
85	1.60/0.20	1.00/0.70	1.40/2.30	3.20/4.50	2.60/2.90	0.40/0.80	0	0	0	0	0	0	0	0	0	0
90	1.40/0.10	1.10/1.00	1.40/2.00	2.60/4.60	2.40/3.10	0.60/0.30	0	0	0	0	0	0	0	0	0	0
95	1.20/0.10	1.40/0.30	1.20/2.90	2.50/2.20	2.10/0.70	1.00/0.10	0	0	0	0	0	0	0	0	0	0
100	1.20/0.01	1.20/0.90	1.60/1.60	2.10/2.10	1.90/1.60	1.40/0.70	0	0	0	0	0	0	0	0	0	0
105	1.30/0.02	1.00/0.01	1.60/0.60	1.80/4.10	2.10/2.40	1.50/0.70	0	0	0	0	0	0	0	0	0	0
110	1.40/0.06	1.00/0.70	1.60/0.60	1.70/3.80	2.00/3.10	1.70/1.40	0	0	0	0	0	0	0	0	0	0
115	1.40/0.40	1.00/0.10	1.50/0.70	1.80/2.20	1.80/1.50	1.70/0.80	0	0	0	0	0	0	0	0	0	0
120	1.50/0	1.00/0.10	1.50/0.30	1.80/2.00	1.70/2.10	1.70/1.40	0	0	0	0	0	0	0	0	0	0
125	1.20/0.40	0.90/0.40	1.40/0.70	2.00/0.50	1.60/0.90	1.60/0.80	0	0	0	0	0	0	0	0	0	0
130	1.40/0	1.00/0.01	1.30/0.30	2.00/0.80	1.40/0.80	1.40/1.00	0	0	0	0	0	0	0	0	0	0
135	1.00/0.03	1.00/0.20	1.50/0.20	1.80/1.40	1.10/1.70	1.20/1.50	0	0	0	0	0	0	0	0	0	0
140	0.04/0.10	1.20/0.70	1.50/1.50	1.80/1.70	0.80/1.60	1.20/1.00	0	0	0	0	0	0	0	0	0	0
145	1.10/0	0.70/0	1.80/0	1.70/0	1.10/0	1.20/0	0	0	0	0	0	0	0	0	0	0
150	1.80/0.10	0.60/0.40	1.60/1.20	1.80/3.10	1.20/3.50	1.10/1.10	0	0	0	0	0	0	0	0	0	0
155	1.40/0	0.70/0	1.40/0	2.10/0	1.00/0	1.00/0	0	0	0	0	0	0	0	0	0	0
160	1.10/0.10	0.80/0.20	1.20/0.80	2.00/0	1.00/0.80	1.00/0.20	0	0	0	0	0	0	0	0	0	0
165	1.30/0.50	0.00/0.90	1.00/1.00	2.30/1.60	1.00/1.70	0.90/0.80	0	0	0	0	0	0	0	0	0	0
170	1.50/0	0.80/0	1.4/0	1.70/0	1.00/0	0.60/0	0	0	0	0	0	0	0	0	0	0
175	1.40/0.50	0.90/1.40	1.20/2.70	2.00/2.80	1.20/1.70	0.50/1.40	0	0	0	0	0	0	0	0	0	0
180	1.40/0	1.30/0	1.14/0	1.70/0	1.10/0	0.60/0	0	0	0	0	0	0	0	0	0	0
185	1.20/0	1.00/0	1.40/0	1.50/0	1.00/0	0.60/0	0	0	0	0	0	0	0	0	0	0
190	1.50/0	0.80/0	1.10/0	1.40/0	1.10/0	0.80/0	0	0	0	0	0	0	0	0	0	0
195	1.70/0	0.90/0	1.30/0	1.40/0	1.40/0	0.70/0	0	0	0	0	0	0	0	0	0	0
200	1.90/0	0.90/0	1.20/0	1.90/0	0.90/0	0.70/0	0	0	0	0	0	0	0	0	0	0

P=Predicted 0=Observed

*No trees larger than 69.999 cm DBH were recorded in the validation data or model runs.

proportion of introduced trees dies from suppression before reaching 2.5 cm DBH. The overestimations in these diameter classes are not serious, as trees of these sizes probably would have been ignored in the Alberta Forest Service permanent sample plot measurements (R. Morton, personal communication).

It is interesting to note that after about year 135, the model predicts a slight increase in number of trees in the 0-2.499 cm diameter class. This corresponds to the period in which basal area of white spruce declines, which improves conditions for establishment and survival of the relatively tolerant white spruce. The effects of stand opening reach the 2.5-4.999 cm diameter class by about year 150, but in reduced proportion to the 0-2.499 cm class. The same general trends are visible in the observed plots.

The 5.0-9.999 cm diameter class shows isolated cases of under or over-prediction of more than 1.0 tree. These instances correspond directly to age classes in which predicted basal area of white spruce is, respectively, lower and higher than observed basal area. The only exception to this is year 80, which shows over-prediction of 1.1 trees. Neither the predicted nor the observed stands show any response to the decline in white spruce basal area after year 135, likely because mortality due to suppression outweighs the effects of increased ingrowth before diameters of 5.0 cm are reached.

In the larger diameter classes, only the 10.0-19.999 cm class shows periods of noticeable difference between observed and predicted numbers of trees. These are: over-prediction of between 2.0 and 3.0 trees in years 55 to 65, and similar under-prediction in years 105 and 110. This diameter class also records over-prediction of 2.0 trees at year 160, and under-prediction of 2.0 trees at year 90. The 20.0-29.999 cm diameter class shows under-prediction of 2.3 trees at year 150. With five exceptions, over or under-prediction of 0.5 or more trees occurs in cases where predicted basal areas are, respectively, lower and higher than observed basal areas. Of these exceptions, only year 65 in the 10.0-19.999 cm diameter class shows a difference of greater than 1.0 tree.

After about year 135, the predicted and observed stands tend to show slight decreases in numbers of trees in all diameter classes between 10.0 cm and 49.999 cm. Numbers of trees in the 50.0-59.999 cm class tend to remain relatively constant. The long-term model predictions show a reversal of all decreases in numbers of trees by about year 230, and a reversal of the increases in the 0-2.499 and 2.5-4.999 cm classes that began after year 135. Subsequently, all diameter classes exhibit cycles of moderate fluctuation in number of trees, with most cycles originating in the 0-2.499 cm class, and moving up into the larger classes with the passage of time. These cycles tend to follow oscillations in basal area. As the magnitude of fluctuation in numbers of

trees is less in the 30.0-39.999 and 40.0-49.000 cm diameter classes, it would seem that old-age stands will generally be dominated by larger trees. Seventeen trees grew into the 50.0-59.999 cm class, two of which grew into the 60.0-69.999 cm class.

Biomass

Figure 13 shows the predictions of JABOR for accumulation of biomass of white spruce.

Biomass shows a rather steep rate of accumulation until about year 125. There is little change up to year 145, with a maximum of 1668 kg recorded at year 140 (1667 kg are present at year 135). This is followed by an erratic decrease to year 210. Subsequently, spruce biomass shows cycles of rather wide oscillation. Accumulation of white spruce biomass follows the same pattern as accumulation of basal area.

C. TOTAL PLOT

Basal Area

Figure 14 shows predictions for total plot (white spruce plus trembling aspen) basal area, compared to observed values.

The observed values exhibit the combined peculiarities of the validation data for white spruce and trembling aspen.

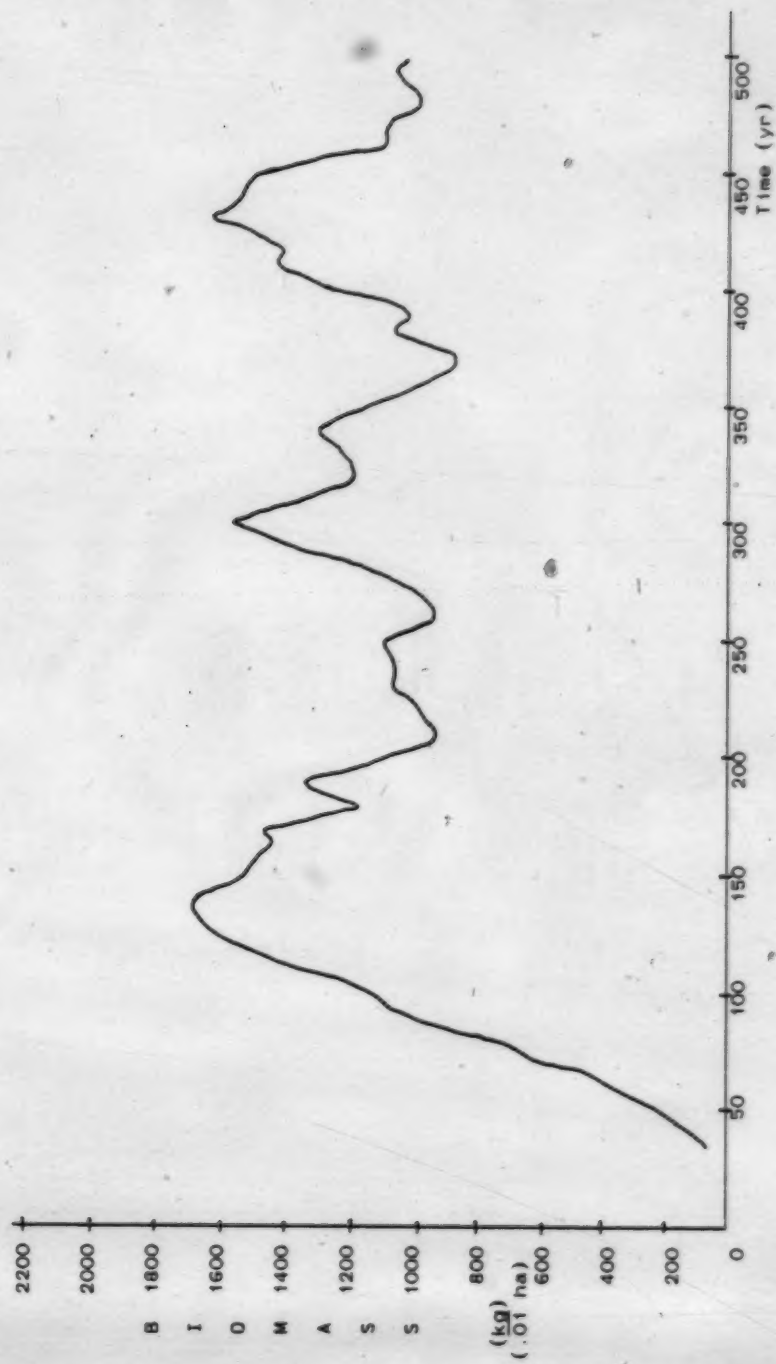


Figure 13. Predictions of average biomass by age class for white spruce between 30 and 500 years.

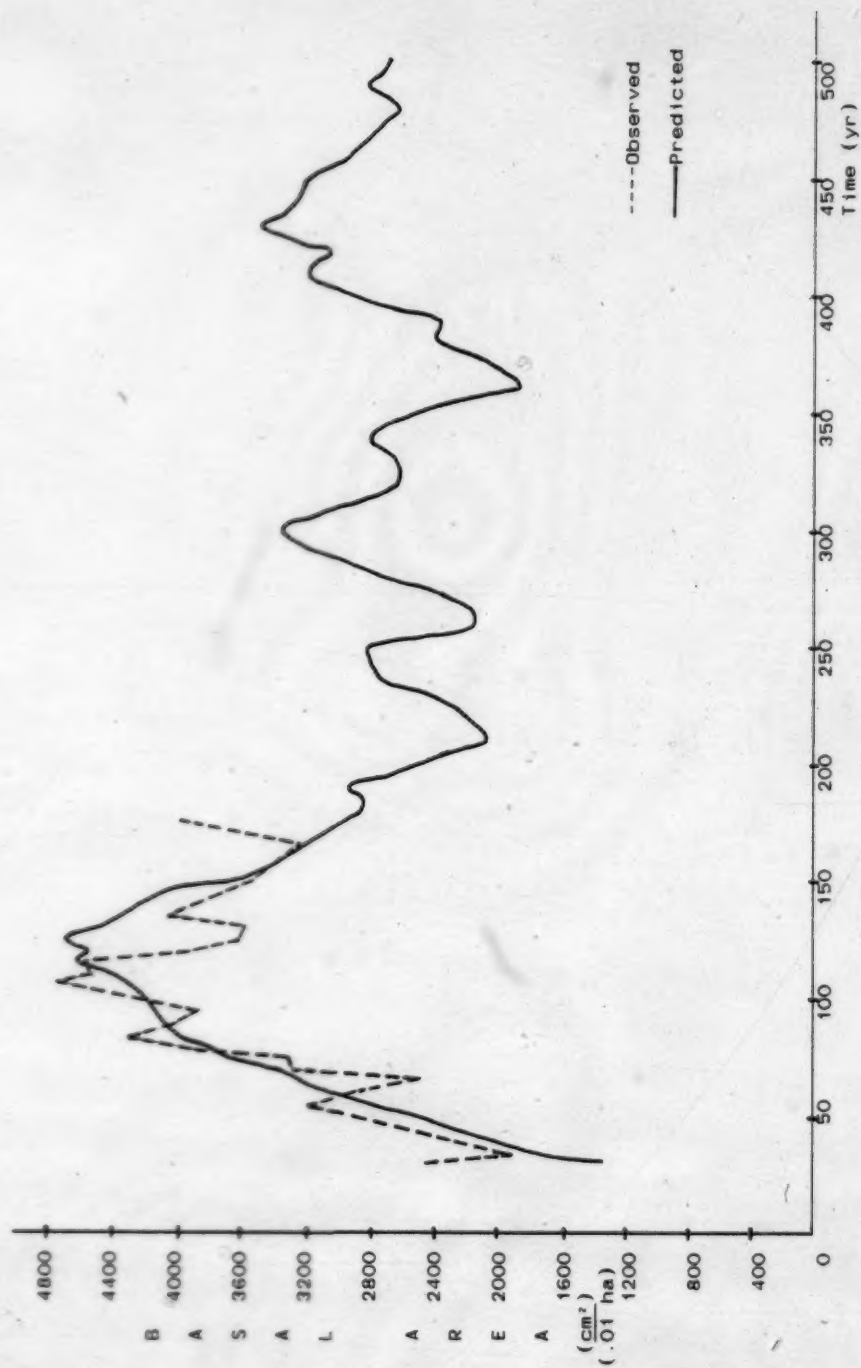


Figure 14. Comparison of JABOR predictions of average total plot basal area by age class to average basal area values of the validation data, plus JABOR predictions between 210 and 500 years.

If observed white spruce basal area at year 175 is viewed as being high, predicted total plot basal area shows a generally good fit to the observed values.¹³ Predicted peak plot basal area occurs at year 125, although there is little fluctuation between years 115 and 130. Due to the basal area contributed by trembling aspen, predicted peak plot basal area occurs somewhat earlier than the predicted peak for basal area of white spruce.

Table A.4.1 of Appendix IV indicates that predicted basal area of white spruce contributes an increasing proportion of predicted plot basal area until about year 170, after which it comprises almost all of plot basal area. Table A.4.1 also shows that predicted plot basal area contributed by trembling aspen decreases steadily after about year 65, and that aspen is present only as a minor constituent after about year 130. It is possible that the model overestimates basal area of trembling aspen during a large portion of the period between years 200 and 500, and trembling aspen may contribute less basal area to old-age white spruce-trembling aspen stands than the model predictions indicate.

Frequency

Figure 15 shows predicted total plot frequencies, compared to observed values.

¹³Except where more specificity is required, the phrase "total plot" is interchangeable with "plot".

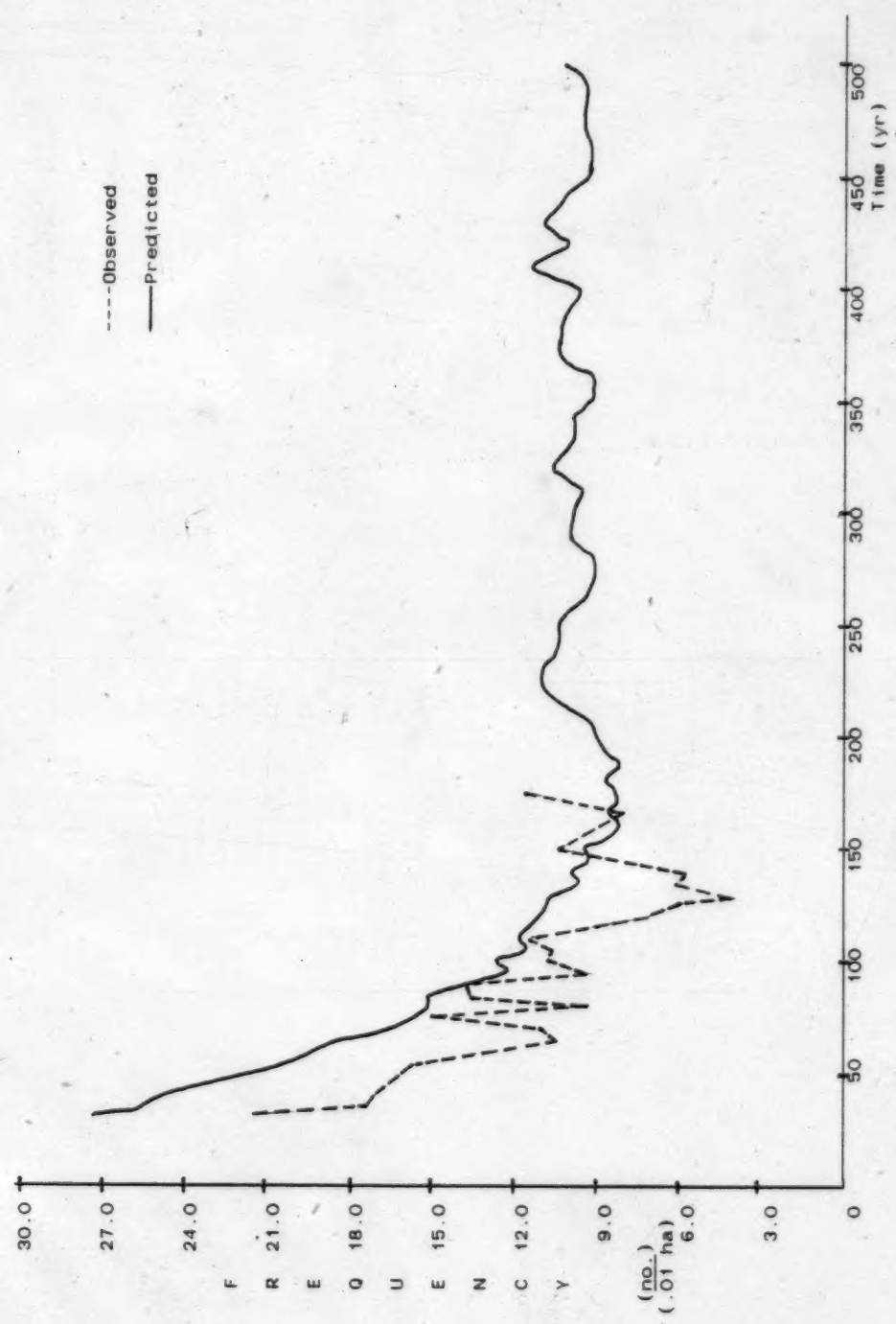


Figure 15. Comparison of JABOR predictions of average total plot frequency by age class to average frequencies of the validation data, plus JABOR predictions between 210 and 500 years.

Observed plot frequencies show a pattern of overall but erratic decline with time, especially if white spruce frequency at year 175 is viewed as being high. The model consistently overestimates plot frequencies, due to over-prediction of numbers of white spruce in the 0-2.499 cm diameter class. However, the model duplicates the general pattern shown by the observed stands.

The model predictions, as shown in Figure 15 and Table A.4.2 of Appendix IV, give a good representation of species population dynamics on upland white spruce-trembling aspen sites. At year 30, there are approximately 27 trees present, approximately 20 of which are trembling aspen. Between years 30 and 105, plot frequency declines to approximately 12 trees. During this period, white spruce frequency increases until about year 45 and then remains relatively constant, and does not compensate for the rapid decrease in trembling aspen frequency. Subsequently, the rate of decline of plot frequency lessens, due to a less rapid decrease in number of trembling aspen. After about year 130, white spruce comprises almost all of plot frequency. As a number of plots move into overmaturity and experience break-down, white spruce ingrowth does not compensate for the decline in number of larger trees, and there is a gradual decrease in white spruce frequency. At year 160, a minimum plot frequency for the 500-year period is recorded, as trembling aspen shows a minimum frequency of 0.30 trees, and white spruce experiences a simultaneous downward fluctuation in

number.

After year 160, trembling aspen is a very minor constituent, showing two periods of relatively minor increase, and subsequent decreases. White spruce continues to gradually decrease in number until year 190, and then shows cycles of relatively minor fluctuation. Total plot frequency continues to exhibit basically the same pattern as white spruce frequency.

Biomass

Figure 16 shows predictions for total plot biomass accumulation. There are no data readily available with which to quantitatively verify the model predictions, so the following discussion is mainly qualitative.

The pattern of living biomass accumulation produced closely resembles that put forth in the Shifting-Mosaic model of Bormann and Likens (1979a,b). Living biomass shows a steady increase until a maximum of 2315 kg is attained at year 120 (2309 kg are present at year 125). Subsequently, there is a relatively smooth decline to year 210, and then a series of rather wide oscillations corresponding to those shown by white spruce biomass, which comprises almost all of plot biomass after about year 170.

The species-specific patterns of biomass accumulation offer the best explanation of why the Shifting-Mosaic pattern would apply to upland white spruce-trembling aspen sites. Peak plot biomass is attained during a period when

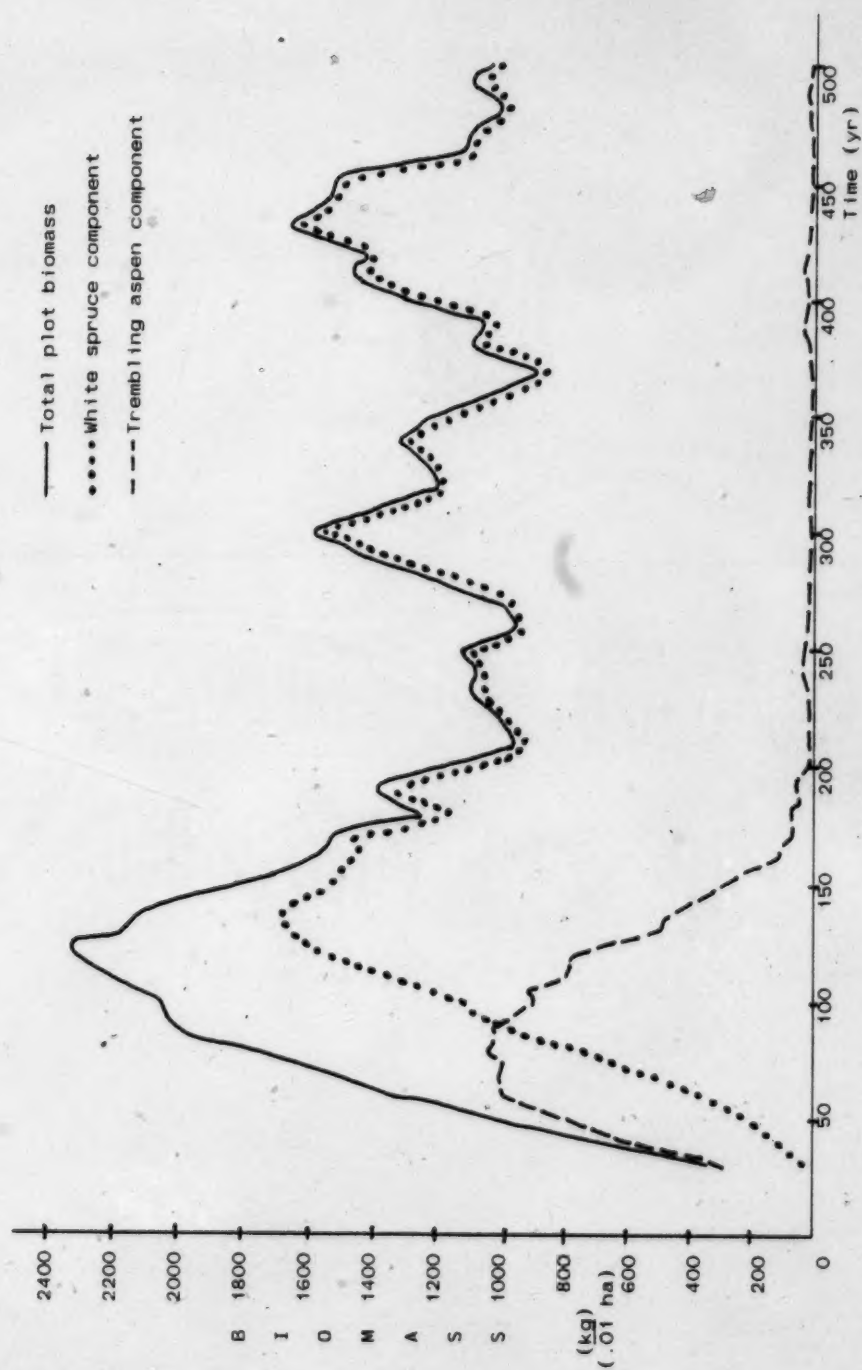


Figure 16. Predictions of average total plot biomass by age class between 30 and 500 years.

large-sized trembling aspen are present in a sufficient number of runs to contribute sizeable quantities of biomass. Also, peak plot biomass occurs only 20 years before white spruce biomass reaches a maximum for the 500-year period. By year 210, when white spruce biomass begins to show a recovery, trembling aspen has become a minor plot constituent, and is present in relatively small sizes. Although white spruce biomass subsequently approaches the species-specific maximum attained in year 140, trembling aspen contributes such a small amount of biomass that plot biomass remains much below the peak recorded at year 120.

It is not altogether surprising that the Shifting-Mosaic model applies to upland white spruce-trembling aspen sites. Shugart and West (1981) found this general response in simulated forests with low species diversities, or where the important species have similar growth rates and longevities. By way of contrast, in diverse forests characterized by species with dissimilar growth rates and life-spans, there is much less synchrony of growth, and the biomass peak may be lost, or delayed into the climax or steady state phase. In such cases, accumulation of living biomass may resemble the asymptotic model. This situation has been shown to occur in long-term simulations of tropical forests (Doyle 1981). Biomass accumulation may also vary from the general pattern predicted by the Shifting-Mosaic model in relatively diverse forests where the first species to colonize after a

7

disturbance may be different from the one(s) dominant in the intact forest. In these cases, the timing and magnitude of the biomass peak may vary substantially as could the point at which the Shifting-Mosaic Steady State phase begins. This has been shown to occur in simulations of mixed pine-oak forests in Arkansas (Mielke et al. 1978).

Bormann and Likens (1979a,b) said that in the northern hardwood forest, a state of maximum biomass occurs because even-agedness after clear-cutting imposes synchrony on all the patches comprising the ecosystem, causing most patches to perform in unison. It is only after a considerable period of time that more or less random forces of mortality bring about an asynchronous and uneven-aged condition. Many studies indicate that historically, the boreal forest has exhibited irregular, but relatively short, cycles of disturbance and regrowth, with fire being the predominant agent of disturbance (Dix and Swan 1971; Kelsall et al. 1977; Alexander and Euler 1981). The regularity with which fire occurs in the boreal forest ensures that the majority of stands within the ecosystem are even-aged, increasing the probability that living biomass accumulation in such stands will follow the Shifting-Mosaic model.

It is probable that in the presettlement era, only in rare instances did any stands or communities reach the climax stage (Loucks 1970; Dix and Swan 1971; Kelsall et al. 1977). This would mean that, on the whole, the process of living biomass accumulation would have been regularly



disrupted, often before peak accumulation would have occurred. While man has greatly reduced the impact of naturally-occurring fire in the boreal forest, he has to an extent compensated for this through settlement, harvesting, and man-caused fires. Climax or steady state forests are therefore still a relatively rare occurrence.

It is an interesting ecological aspect of the model predictions that peak biomass for the white spruce-trembling aspen stands occurs at year 120,¹⁴ while in the northern hardwood forest, the peak occurs at about year 170 (Bormann and Likens 1979a). The primary reason for this lies in the differences between longevities of the species that dominate the latter stages of succession in each ecosystem. For example, of the species used in JABOWA, red spruce, beech, yellow birch, and sugar maple are the longest-lived, with respective maximum ages of 350, 300, 300, and 250 years. Only two of the remaining nine species have AGEMX values greater than or equal to 100 years. At lower to middle elevations, beech is the dominant tolerant species in the latter stages of succession, and sugar maple tends to be next in importance. Although yellow birch is relatively intolerant and declines steadily in frequency after the earlier stages of succession at these elevations, it contributes the most basal area until well after year 200. It is therefore also a dominant species in the latter stages

¹⁴The timing of this would, of course, vary in a minor way with a different number of runs, or use of a different data set.

of succession. At higher elevations, red spruce is the dominant species after about 100 years. In JABOR, white spruce is the dominant species in the latter stages of succession, and has an AGEMX of 250 years. In both models, the probability of any tree living to the maximum age for that species is very low, especially in JABOR, where size-dependent mortality progressively increases the chance of death after a tree reaches 34.0 cm DBH. The end result is that on the majority of the plots, during the latter stages of succession, the largest trees of the dominant species will die off long before the respective AGEMX values are approached, and this shifts the point of peak biomass substantially ahead of these values. Since the late-successional dominant species in JABOWA are relatively longer-lived than white spruce, peak biomass in the boreal stands occurs accordingly earlier than in the northern hardwood forest.

It should be pointed out that the size-dependent mortality function used in JABOR does not appear to have an important effect upon the actual timing of the predicted point of peak living biomass. By year 120, the majority of the model runs show white spruce and/or trembling aspen trees with DBH's greater than or equal to 34.0 cm, the diameter at which size-dependent mortality first shows an increase for both species. However, it is not until after year 130 that size-dependent mortality seems to have any visible effect upon the death rates of either species. It

therefore appears that the initial decline in biomass is due primarily to random deaths of the largest trees on the simulation plots.

As the JABOR model does not include calculation of volume, little can be said about potential conflicts in forest management schemes that would incorporate concurrent utilization of fibre and biomass. At one point, the assumption was made that basal area could be used as a reasonable approximation of volume. The JABOR predictions show maximum mean annual increment (MAI) of white spruce basal area at year 115, of trembling aspen basal area at year 45, and of total plot basal area at year 40. Maximum MAI of biomass occurs at year 125 for white spruce, and at year 60 for trembling aspen. Total plot biomass shows maximum MAI at year 85, although there is a range of only 0.51 kg/yr in values recorded between years 60 and 90. It was felt that the differences in timing of maximum MAI values for corresponding basal area and biomass components should not be as wide as the model predictions indicate (K. O. Higginbotham, B.L. Phillips, personal communications). It is therefore possible that basal area is not a reasonable approximation of volume, or that the biomass equations of JABOR produce a degree of inaccuracy when applied to young-aged stands. Further investigation is required to determine which of these is the causative factor.

It should be pointed out that when considering the pattern of living biomass accumulation that is predicted by

the JABOWA and JABOR growth models, the effects of model structure must be taken into account. There is a definite possibility that the predicted pattern would be inherent to an individual tree-based growth model, and especially one in which tree mortality is based on a relatively simplistic function such as the one used in JABOWA and modified only slightly for use in JABOR. Until data become available with which to verify the biomass predictions of the JABOR and JABOWA models, this question cannot be conclusively answered.

D. GENERAL ASSESSMENT OF THE MODEL

As was the case with the JABOWA simulator, the JABOR model demonstrates that an accurate and valid description of a forest ecosystem can be developed at a level that does not include microscopic detail. In addition, the overall flexibility of the model increases its usefulness for investigating the influences of various ecological factors, processes, and phenomena upon the relative importance of species in the simulated stands.

Holdaway and Brand (1981) and Buchman and Shifley (1983) have stated that all forest growth models are at best a simplification of extremely complex biological and ecological processes, and are subject to imperfections and irregularities. Most of the imperfections within the results of JABOR are due to shortages of relevant and precise data for the western Canadian boreal forest. In almost all

aspects, there is a critical paucity of data for white spruce-trembling aspen stands younger than 40 years of age, and especially those less than 30 years. Conclusive data for stands 150 years and older are also limited.

A more specific area in which a critical data shortage existed concerned processes and rates of birth and mortality of white spruce and trembling aspen, and of species eliminated from the model. The major problems arising from these shortages are:

1. The function for introduction of trembling aspen to open sites is a very weak aspect of the model.
2. As only zero or one white spruce sapling(s) can be added to a plot each year, spruce cannot enter a plot in large numbers when stand density is low. For example, if introduction of trembling aspen is reduced or prevented in simulations beginning with bare-ground conditions, the user must interactively input estimates of white spruce saplings for at least the first year.
3. The long-term predictions of the model probably overestimate rates of introduction of trembling aspen into old-age mixedwood stands.
4. Until more is known about rates of seedling and sprout establishment and survival in all stand ages, trees cannot be input to a plot at less than sapling size.
5. The size-dependent mortality function remains simplistic and unrefined, with no differentiation among agents of mortality.

6. While the growth-dependent mortality function appears to be a very positive aspect of the model, much more data regarding numbers and survival rates of trees in the smaller diameter classes are needed for verification of the model predictions.

Within the validation data used, none of the permanent sample plots used has a period greater than 22 years between initial and final measurements. Therefore, very little insight can be gained regarding the history and development of any of the observed stands. The "composite" successional sequence of observed stands that is used does not represent a real-life successional sequence, and is a less than perfect basis upon which to verify the model results.

No validation data were available for years 50, 145, 155, and 170, only three plots were available for years 135 and 165, and one was available for years 45 and 160. Consequently, there is wide disparity between number of validation plots per age class. The possibility of variation in observed basal area, frequency, and diameter distributions between age classes is greatest when only a small number of validation plots are available for an age class. In these cases, any irregularities or peculiarities will not be averaged into a larger data set. This is especially so when all validation plots for an age class are from the same permanent sample plot group, as occurred in years 135, 160, and 165. All validation data for years 90, 100, 125, and 135, and one-half of the data for year 120,

were remeasurements of Alberta Forest Service permanent sample plots. In such instances, the data could be subjected to irregularities or bias in the initial measurement.

Another weak aspect of the validation data is the questionable accuracy of the number of trees recorded in the 0-10.0 cm size classes, especially for white spruce. Accurate data on ingrowth and regeneration of all species concerned is vital to realistic simulation. On the positive side, the validation data were obtained from sources entirely different from those used in collecting program data.

A lack of relevant data often necessitated use of general or unproven values for the program parameters that define species characteristics. Values for DBHMAX, HTMAX, AGEMX, and DMAX are at best reasonable approximations. The WMAX values could be much more precise, although this parameter is used only in determining whether a species can grow under the prevailing soil moisture conditions, and the JABOR model assumes that soil moisture is not a limiting factor on any sites. Data for the relationship between leaf weight and tree diameter were very weak for both white spruce and trembling aspen. If local leaf biomass equations were available for white spruce and trembling aspen, accuracy of values for C (leaf-area constant) and F (exponent in the leaf-weight equation) may have been increased. Prediction of total-tree biomass below the species-specific diameter limits imposed by the equations of

Singh (1982) should be improved. The possibility that the biomass equations used produce a degree of inaccuracy in young-aged stands should be investigated, and if necessary, corrected. If biomass equations for the various tree components, including roots, were available, the usefulness of the model in evaluating forest ecosystem productivity would be increased.

It is well-known that derivation of appropriate mathematical relationships which accurately describe the complex biological processes inherent in a forest ecosystem is one of the most difficult aspects of growth model construction (Holdaway and Brand 1981). Also, when developing a forest growth model such as JABOR that is primarily a modification of another model, there are definite constraints imposed by the structure, assumptions, and mathematical relationships of the original model. Consequently, some of the relationships and equations developed for use in JABOWA, and included in the JABOR model, are at best general approximations of real-life phenomena. As explained, the relationship between leaf weight and tree diameter is one of the weakest components of JABOR, as well as JABOWA (Botkin et al. 1972a,b). Reed (1980) pointed out that this relationship may be reasonable for application to hardwood species, but that a somewhat different principle may apply to conifers, most of which retain their leaves for one or more growing seasons. Botkin et al. (1972a) have indicated that the JABOWA model is not

as sensitive to changes in the photosynthetic rate versus available light relationship as it should be, and Botkin (1974) stated that the algorithms used in determining the effects of temperature and soil moisture upon tree growth should be more attuned to actual physiological processes. As these three relationships were not altered for use in the boreal version, they remain as weak aspects of the JABOR model.

Botkin (1974) stated that tree growth could be made less deterministic by generating a degree-day value for the plot as a stochastic value. A degree of random variation in the species-specific growth constants would also make tree growth less deterministic, and reflect genetic differences between trees, changes related to life cycle stages, or variations in micro-environment (K. O. Higginbotham, B.L. Phillips, personal communications).

Certain abiotic elements of the model should also receive attention. Values for TILL (average soil depth), TEXT (average amount of soil available for water storage), and EXCESS (fraction of precipitation available for evapotranspiration) that are specific to the western Canadian boreal forest should be obtained. Also, the model was not applied to other sites and locations within the western Canadian boreal forest.

E. POSSIBILITIES FOR EXTENSION OF THE MODEL

The usefulness and applicability of the JABOR model could be increased in a number of ways. First and most obvious is the inclusion of more upland mixedwood tree species. Once the timing of the entrance of balsam fir can be determined with more precision, and more is known about the nature of the interactions between fir and white spruce, the species could be incorporated with relative ease. It is possible that a program function similar to the one used for introduction of white spruce would effectively simulate the reproductive mechanisms of balsam fir. JABOR contains an R(AL) factor (reduction of diameter growth due to shading) for very tolerant species, such as balsam fir, that was included in Version II of JABOWA.

Once sufficient data are available, species that tend to be minor constituents of mixedwood sites, such as balsam poplar or white birch, could be incorporated. Species introduction could be modelled by adding small numbers of trees on a random basis. The possibility that such species could be present as the main constituent(s) of a plot could be included, by an algorithm that chooses colonizing species based on probability levels.

Inclusion of hydric and xeric sites, and appropriate species, should also be a priority. This would require modification of the subroutines dealing with calculation of site characteristics, determination of introduction of species and number of trees per species, and calculation of

tree growth. In determination of site soil moisture, additional factors such as depth to water table, soil texture (for example, organic, clay, or sand), and inflow or outflow of water (in larch fens, for example), would need to be included. An algorithm that eliminates tree species that cannot grow under the prevailing moisture conditions, similar to that presently used in JABOR, could be retained. However, many boreal species can establish and grow under a wide range of soil moisture conditions (Larsen 1980). Therefore, biasing of species introduction, and number of trees introduced per species, according to moisture conditions and species characteristics, would be necessary. The effects of soil moisture upon tree growth could be determined in a similar manner. As moisture conditions deviate from those required for optimal growth of a species, diameter growth would be progressively reduced.

It is probable that the modifications outlined here could be incorporated using assumptions and mathematical relationships that are consistent with the generally simplistic nature of JABOR. It is also probable that the mortality functions used in JABOR could be retained. As simulations would include stands with only one or two species, it is possible that biasing of diameter distributions toward the larger diameter classes, as was encountered in trial runs of JABOR, would occur. Therefore, it is unlikely that the diameter limits and probability levels used in the size-dependent mortality function would

be eliminated.

Algorithms modelling cycling of nutrients would provide additional insight into the factors affecting tree growth, and into the biogeochemistry of boreal upland mixedwood sites. Equations for calculation of stand and tree volume would increase the usefulness of the simulator for forest management-oriented purposes, and would be easy to include. For long-term simulations, it would be useful to include treatment of species migration in response to climatic fluctuation. Botkin et al. (1972b) stated that long-term changes in growing degree-days can be adequately modelled, but that modification of JABOWA to include species migration has not yet been attempted.

As more pertinent data become available for the western Canadian boreal forest, the accuracy and applicability of later versions of the JABOR model will be directly increased. A useful tool in overcoming the data and information shortages that have been discussed would be permanent sample plots which are established as soon after stand origin as possible, and then monitored closely through all stages of development. There are, of course, many difficulties associated with such an undertaking, including the large time-scale involved.

VI. FOREST MANAGEMENT APPLICATIONS OF THE MODEL

The JABOR model can be used to investigate a wide range of forest management topics and subjects. Some examples are:

1. Effects of different harvest methods, such as clear-cut versus selection or shelter-wood.
2. Effects of various thinning and release treatments upon species and stand growth.
3. Effects of species conversion and/or manipulation, through manual removal, or by the use of chemicals.
4. Effects of various planting and regeneration treatments:
 - a. During stand development
 - b. After harvest or disturbance
5. Effects of increasing the growth rate of a species, through:
 - a. Fertilization or tree improvement
 - b. Improvement of site quality
6. Effects of increasing:
 - a. Life-span of a species
 - b. Temperature ranges under which reasonable and/or optimal growth can occur
 - c. Shade tolerance
7. Testing of alternatives for management of overmature stands

The JABOR model was tested against two field studies dealing with the effects upon growth of white spruce of: removal of trembling aspen competition (Lees 1966), and selective cutting of trembling aspen and white spruce

(Steneker 1974). The model was also applied to a topic which has not been previously investigated: the response of white spruce to complete removal of trembling aspen at various stand ages. These topics were chosen because there is much opportunity for research into the effects of thinning and/or release treatments in the western Canadian boreal forest (Dempster 1983).

A. CASE STUDY I: Steneker (1974)

1. Field Study Procedure:

- a. The purpose of the field study was to determine the effects of commercial release cuttings in 75 to 100-year old boreal mixedwood (Section B.18a of Rowe 1972) stands upon subsequent growth of residual white spruce. The study was carried out in western Saskatchewan. Two stands were chosen in which the trembling aspen component was at or near maturity, and white spruce had in places broken through the aspen canopy. A study area was established in each stand, and within each study area, four control and four treatment plots were established.
- b. On the treatment plots, basal areas of trembling aspen and white spruce were reduced by about 50 and 30 per cent, respectively. The procedure used was to remove all white spruce in the 25.0-35.0 cm diameter range, along with some good quality trembling aspen, and a few smaller white spruce.

- c. After a ten-year period, trees on all plots were remeasured. One treatment plot from Study Area I could not be used for remeasurement (reason not specified).

2. Case Study Procedure:

- a. For each study area used in the field study, the following values were calculated:
 - i. average basal area for all control plots, by species, for the beginning and end of the observation period.
 - ii. average basal area for all treatment plots, by species, before removal, after removal, and at the end of the observation period.

To ensure consistency with the JABOR model, these basal area values were converted to a 0.01 ha plot size basis

- b. The objective of this portion of the project was to demonstrate the applicability of the JABOR model to field and management-oriented purposes. Therefore, only one set of artificial control and treatment stands was used, as opposed to the two sets used in the field study.

An artificial stand was constructed that produced reasonable approximations of the average initial species basal areas of the control plots of each study area used in the field study, and the average before-removal species basal areas of the treatment plots of each study area. This artificial stand also allowed close simulation of the removal procedures used by Steneker

(1974), and produced after-removal species basal areas that approximated those of the field study treatment plots.

As Steneker (1974) placed very little emphasis on the results for trembling aspen, more detail was given to matching artificial and observed basal areas for white spruce than for aspen. Another reason for this was that observed average basal area for trembling aspen was very much higher in Study Area I than Study Area II, for control and treatment plots. It should be mentioned here that for both white spruce and trembling aspen, the removal procedures used by Steneker, and the small plot size used in JABOR, imposed some limitations upon artificial basal areas that could be obtained, especially after-removal values. On a 0.01 ha plot, removal of one or more white spruce trees in the 25.0-35.0 cm diameter range, or one or more dominant trembling aspen trees, can have a large effect upon species basal area.

- c. The artificial control stand was input into the model, without removal of any trees, and averages of ten stochastic runs of ten-year duration were obtained. This served as the control plot. Next, trees designated for removal were eliminated, and averages of ten stochastic runs of ten-year duration were again obtained. This served as the treatment plot.

3. Results: Table 8 compares the results of the field study

and the simulation runs.

- a. White spruce: On the observed control plots of both study areas, white spruce showed an increase in basal area over the ten-year period. On both sets of observed treatment plots, white spruce showed an increase in basal area after removal, but did not recover to pre-removal levels within 10 years.

These patterns were closely duplicated by the model results. The predicted magnitude of response in basal area is, in all cases, very similar to the field results. For example, the percentage increase in basal area on the simulated control plot was within three to five per cent of the percentage increases on the observed plots. On the simulated treatment plot, percentage decrease from pre-removal to the end of the observation period was within one and three per cent of observed percentage decreases.

- b. Trembling aspen: In the field study, the behavior of trembling aspen varied widely between the two study areas. This is probably due to the rather large differences between the study areas as to average initial basal area on the control plots, and average pre-removal basal area on the treatment plots. On the control plots, Study Area I showed an overall decrease of average basal area of trembling aspen, while Study Area II showed a small increase. On the treatment plots, Study Area I showed a greater decrease in average basal

Table 8. Case study I: comparison of JABOR predictions of response of average basal of white spruce on control and treatment plots to field study results (Steneker 1974).

2 BASAL AREA (cm /0.01 ha)					
OBSERVED:					
STUDY AREA	PLOT	SPECIES	BR	AR	FINAL
I	Control	Sw Aw	2696 1796	2696 1796	3048 1531
	Release	Sw Aw	2074 2180	1506 1108	1722 696
.....					
II	Control	Sw Aw	2920 326	2920 326	3242 350
	Release	Sw Aw	2909 464	2162 200	2536 295

PREDICTED:					
	Control	Sw Aw	2713 1393	2713 1393	3151 1141
	Release	Sw Aw	2713 1393	1898 608	2333 700

LEGEND: Sw: White spruce
 Aw: Trembling aspen
 BR: Before-removal
 AR: After-removal
 FINAL: End of observation period

area from after-removal to the end of the observation period than did Study Area II.

As a result of these differences, it was difficult to accurately simulate the behavior of trembling aspen. However, the simulated control plot showed a response very similar to the observed control plot of Study Area I. Although the simulated treatment plot showed an increase in basal area from after-removal to the end of the observation period, predicted percentage decrease from pre-treatment to the end of the study period was within eight and eighteen per cent of observed percentage decreases.

4. Discussion and Assessment: Steneker (1974) concluded that white spruce in the 70 to 80 year range is too old to respond to release. Despite the rather limited scope and general methodology of this case study, it appears that the JABOR model duplicates reasonably well the results of the field study.¹⁵ However, I feel that, in making his conclusion, Steneker placed too much emphasis on the negative overall response of white spruce basal area on the treatment plots. The possibility exists that the amount of basal area removed was too great to allow recovery within ten years. Further, Steneker's conclusion did not include consideration of basal area removed from the treatment

¹⁵It should be pointed out that the white spruce trees used in JABOR may not fall exactly within the 70 to 80 year range. However, as the JABOR stands closely approximate observed diameters and basal areas of white spruce, it is probable that there is also close agreement between predicted and observed tree ages.

plots. For example, on Study Area I, the control plot showed a 13.1 per cent increase in basal area of white spruce during the ten-year observation period. On the treatment plot, 568 cm² of spruce basal area were removed, and there was 216 cm² of growth over the ten-year period. The total of these two values is 37.8 per cent larger than the pre-removal value. Similarly, on Study Area II, the control plot showed an 11.0 per cent increase in white spruce basal area during the ten-year observation period. However, on the treatment plot, the combination of basal area removed and ingrowth was 38.5 per cent larger than pre-removal basal area. For comparison purposes, the simulated control plot showed a 16.0 per cent increase in white spruce basal area over ten years. On the simulated treatment plot, the combination of basal area removed and ingrowth was 46.1 per cent larger than pre-removal basal area.

The results of this case study suggest that the JABOR model should be widely applicable to upland white spruce-trembling aspen sites within the western Canadian mixedwood boreal forest. A more in-depth case study should include additional sets of control and treatment plots, and closer matching between simulated and observed before-removal and after-removal species basal areas. Also, data for average monthly temperature and precipitation for the field study location were not readily available. Considering the limited objectives of this case study, climatic data for the Whitecourt area were retained. This would not have an

important effect on the simulation results, as there is not a great geographical distance between the Whitecourt and field study areas, and any climatic differences would not be large.

B. CASE STUDY II: Lees (1966)

1. Field Study Procedure: The purpose of the field study was to determine whether removal of trembling aspen competition has an effect upon the growth of white spruce, over a wide range of diameters of white spruce. Twenty-five white spruce-trembling aspen stands of varying age were located near Lesser Slave Lake, Alberta, in the boreal mixedwood forest (Section B.18a of Rowe 1972). A total of 333 individual white spruce trees were released from trembling aspen competition, and measurements of DBH, height, and age were taken. These trees ranged in diameter from less than 2.0 cm to 36.0 cm, with most trees less than 25.0 cm DBH. Ages of trees ranged from less than ten years old to 70 years. A total of 323 control trees that were similar to the released trees in DBH, height, and age was selected. After a ten-year period, those trees that were not lost to road construction or fire were remeasured.

2. Case study procedure:

- a. Simulation runs based on individual trees were not carried out, as this would require time and expense beyond the scope and objective of this portion of the project. Instead, artificial control and treatment

stands were used. The limitations imposed by this methodology upon the results of the case study will be discussed afterward. The artificial control stand contained ten white spruce trees with the following DBH's: 20.0 cm, 18.0 cm, 15.0 cm, 12.0 cm, 9.0 cm, 8.5 cm, 7.5 cm, 5.0 cm, 3.0 cm, and 2.0 cm. Four trees with DBH between 7.5 and 13.0 cm were included because Lees (1966) reported highest diameter increment response by released trees in this size range. The control stand also contained ten trembling aspen trees, with the following DBH's: 22.0 cm, 21.0 cm, 19.5 cm, 19.0 cm, 18.0 cm, 17.5 cm, 17.0 cm, 16.5 cm, 6.0 cm, and 5.0 cm. I felt that this frequency and size distribution of trembling aspen provided a good representation of a mixedwood stand in which white spruce had attained a diameter of 20.0 cm. It also gave good representation of the effects of shading by, and competition from, trembling aspen upon growth of white spruce.

The treatment stand contained ten white spruce trees identical in size to those used in the control stand, and no trembling aspen trees.

- b. The artificial control and treatment stands were input into the model, and averages of ten stochastic runs of ten-year duration were obtained. In these runs, mortality and ingrowth of white spruce were prohibited.
3. Results: Table 9 shows results reported by Lees (1966) for average annual diameter increment for the ten-year

period, for trees ranging in initial diameter from 2.54 cm to 25.4 cm. Table 10 shows predictions of the model, for trees ranging in initial diameter from 2.0 cm to 20.0 cm. As stated, Lees reported the greatest response by released trees with initial diameters between 7.5 cm and 13.0 cm. The model predictions showed greatest response by released trees with an initial DBH of 2.0 cm, but only slightly less response for the trees with initial DBH's of 7.5 cm and 8.5 cm. The latter two tree sizes fall within the 7.5-13.0 cm range reported by Lees.

It can be seen that the average annual diameter increments recorded by Lees (1966) are exceptionally high. The most probable explanation for such growth would be that many sites in the vicinity of the study area exhibit extremely favorable growing conditions (G. H. La Roi, personal communication).¹⁶ It can also be seen that in all cases, predicted values are well below those of Lees, especially for the released trees. To ensure that this was not the result of procedures used in the case study, diameter increments were calculated for individual white spruce trees grown with no other trees present, and therefore no competition for light (R(AL) function), or soil moisture and nutrients (S(BAR) function). A maximum diameter increment of 0.457 cm/yr was recorded, for a tree with a diameter of 25.4 cm. Under optimal climatic conditions (T(DEGD) function), a tree of this size showed a maximum increment of 0.572 cm/yr.

¹⁶G. H. La Roi, Professor, Department of Botany, University of Alberta, Edmonton, Alberta.

Table 9. Case study II: average annual diameter increment of control and treated white spruce trees in field study (Lees 1966).

INITIAL DBH (cm)	AVERAGE ANNUAL DIAMETER INCREMENT (cm/yr)		PERCENTAGE DIFFERENCE
	CONTROL	TREATED	
2.54	0.36	0.58	38
5.08	0.43	0.69	38
7.62	0.48	0.74	35
10.16	0.61	1.11	45
12.70	0.58	0.99	41
15.24	0.66	0.94	30
17.78	0.66	1.12	41
20.32	0.81	1.12	28
22.86	0.61	1.11	45
25.40	0.66	0.99	33
AVERAGE	0.59	0.94	37.4

Table 10. Case study II: predictions of JABOR for average annual diameter increment of control and treated white spruce trees.

INITIAL DBH (cm)	AVERAGE ANNUAL DIAMETER INCREMENT (cm/yr)		PERCENTAGE DIFFERENCE
	CONTROL	TREATED	
2.0	0.25	0.30	17
3.0	0.28	0.32	13
5.0	0.31	0.36	9
7.5	0.33	0.38	14
8.5	0.33	0.38	14
9.0	0.34	0.39	13
12.0	0.35	0.40	13
15.0	0.36	0.41	13
18.0	0.37	0.42	12
20.0	0.37	0.42	12
AVERAGE	0.33	0.38	13.0

Both of these values are less than all average diameter increments of the released trees in the Lees study, and less than most of the average increments of the control trees. It can therefore be concluded that constraints within the model are responsible for the model predictions not matching the diameter growth recorded by Lees.

It should also be mentioned that this case study retained climatic data for the Whitecourt area, and did not utilize data from the Slave Lake area. However, since the model could not match the diameter growth reported by Lees (1966) even under optimal climatic conditions, usage of Slave Lake data would have produced only slightly closer agreement, if any.

4. Discussion and Assessment: Lees (1966) concluded that over a wide diameter range, growth of white spruce increased significantly after release from trembling aspen competition. He also recommended that release of white spruce be carried out before it grows into the trembling aspen overstory, as top damage to white spruce can be extensive in this period. The predictions of the model support the findings of Lees, as the released simulation trees showed increases in diameter increment over the control simulation trees. The algorithms and functions of JABOR do not incorporate the effects of top damage, so that Lees' recommendation as to timing of removal of trembling aspen cannot be conclusively tested.

The fact that the simulation runs showed rather large

quantitative differences from the results of the field study points to a useful feature of the JABOR model. Since the model is geared to respond to average growing conditions, and to predict tree growth for the average upland boreal mixedwood stand, it can be used to indicate or isolate sites where unusual growth occurs. This case study also points out a further limitation of the model, by showing that the simulator cannot be effectively used in stands exhibiting a higher inherent growth rate than that built into the growth rate equation. This in turn points to further possibilities for improvement of the model, in that tree growth could be made more responsive to variations in environmental conditions and site quality, and to the effects of genotypic variation.

It is likely that general approximations of the results obtained by Lees (1966) could be produced through alteration of the G (growth rate constant) parameter for white spruce. This would probably also require altering the value of G for trembling aspen. However, Lees does not include any data on growth of aspen in his study.

It should be emphasized that Lees (1966) recorded the growth and response of individual trees, while the simulation runs had all white spruce trees on one plot. As a result, the smaller white spruce trees would have been shaded by larger spruce trees, and subjected to additional reductions in diameter growth. The effects of competition, through relatively higher levels of competing basal area on the

plots, would also have been increased. However, it has been demonstrated that even without the effects of these reducing factors, the model could not have produced growth and/or response of white spruce anywhere near that reported by Lees.

A more in-depth case study should include individual tree-based simulation runs, and testing of the response of a greater number and range of tree sizes. However, such improvements could lead to substantial increases in expense.

C. CASE STUDY III: Investigation of Hypothetical Topic

1. Objective: To determine at which stand age or ages complete removal of trembling aspen from a plot results in the greatest increase in growth of white spruce.

2. Case study procedure: Sets of 20 simulation runs beginning with bare-ground conditions were carried out, in which the plots were subjected to complete removal of trembling aspen at a specific stand age. A set of 20 control runs, which also began with bare-ground conditions, were selected at random from the 25 runs discussed in "RESULTS AND DISCUSSION". All simulation runs were of 150-year duration. In each set of runs, basal area accumulation of white spruce was monitored, and averages were obtained at ten-year intervals.

In the first set of treatment runs, trembling aspen was removed at year 30. In each subsequent set, age of removal was increased by ten years, up to a maximum of 110 years.

After this point, trembling aspen was not present in a sufficient number of plots to allow conclusive testing. As no validation data were available for stands less than 30 years of age, treatment at years 10 and 20 were not tested. A set of runs in which introduction of trembling aspen was initially prohibited was also carried out, but since the model introduces very low numbers of white spruce to open sites, the results of this treatment must be viewed with caution. A lack of reliable data on initial frequencies of white spruce on plots free of trembling aspen prevented inputting of artificial frequencies. Estimates were not used, as the results would have still been very tentative in nature, and the reliability of the predictions for treatment at this age would not have been substantially increased.¹⁷

3. Results: Table 11 shows, for each treatment age, average accumulation of basal area of white spruce over time, year of maximum average basal area, and year of maximum mean annual increment (MAI) of average basal area.¹⁸

All treatment ages up to and including year 90 show substantial increases in basal area of white spruce over the control plot, at variable lengths of time after removal of trembling aspen. It should be noted, however, that for treatment at year 70, basal area of white spruce had

¹⁷Estimates of frequency based on recommended planting spacings were not considered for use. While such estimates would be useful in a planting-oriented case study, they have marginal value for thinning or removal treatment-oriented studies.

¹⁸A complete listing of values for MAI of average basal area per stand age per treatment age is included in Appendix V.

Table 11. Case study III: predicted average basal area of white spruce per age of removal of trembling aspen; plus year of maximum average basal area of white spruce per age of removal, and year of maximum mean annual increment of average basal area of white spruce per age of removal.

AVERAGE BASAL AREA (cm ²)												
		Age of Treatment (yr)										
		CONTR	0	30	40	50	60	70	80	90	100	110
	30	165.3	172.4	143.5	141.9	150.0	157.6	169.0	145.3	168.7	210.7	169.2
	40	389.4	353.5	352.4	309.3	345.1	319.2	376.5	321.6	344.1	412.7	380.2
S	50	685.0	685.8	643.2	603.9	599.6	557.5	628.9	540.6	628.7	564.9	665.7
T	60	1038.4	1108.9	1049.2	936.0	954.3	917.1	983.4	864.5	942.4	812.8	1068.3
A	70	1381.6	1644.9	1554.6	1492.3	1510.6	1365.4	1446.2	1264.0	1333.6	1127.6	1435.5
N	80	1879.2	2272.8	2121.8	2132.9	2018.6	1958.8	1969.6	1655.7	1617.8	1452.1	1759.8
D	90	2300.1	2821.2	2811.9	2610.9	2534.9	2404.5	2392.9	2152.2	2209.8	1901.5	2277.1
G	100	2560.8	3469.8	3325.1	3113.9	3014.0	2888.8	2882.4	2731.5	2685.9	2278.9	2668.4
E	110	2917.3	3733.9	3585.0	3753.4	3322.3	3412.5	2960.8	3342.6	3234.1	2695.2	2825.8
Y	120	3146.9	3814.1	3857.0	3953.9	3602.5	3724.5	3432.8	3769.6	3683.1	2916.5	2897.3
R	130	3476.7	3954.2	4093.4	3820.2	3298.3	4047.5	3747.8	4300.7	3313.7	3054.4	2989.4
	140	3398.0	3973.5	3968.5	3857.1	3510.8	3985.8	3881.9	4227.3	3485.2	3032.8	3165.1
	150	3101.6	4014.0	3614.0	3787.6	3316.9	3738.1	3269.2	4096.9	3550.5	3117.8	3198.5
YR. OF												
MAX. BA	130	150	130	120	120	130	140	130	120	150	150	
YEAR OF												
MAX. MAI	130	100	100	110	110	130	130	130	120	110	100	

exceeded the control plot value before removal was carried out. Treatment at years 100 and 110 resulted in only slight increases in basal area of spruce over the control plot.

The year at which maximum basal area is attained varies between years 120 and 150, with no visible relation to year of treatment. The year at which maximum MAI occurs tends to increase with treatment age, up to and including treatment at year 60. At this treatment age, maximum MAI occurs at year 130, the same as for the control plot, and treatment at years 70 and 80. Year 130 was the latest point at which a maximum MAI occurred, while the earliest was at year 100, for treatment at years 0 and 30.¹⁹

4. Discussion and Assessment: Based on the results of this case study, it would appear that complete removal of trembling aspen causes increases in accumulation of basal area of white spruce after removal, up to at least a treatment age of 90 years. However, due to variability within the results, caused by the influence of stochastic factors within the model, it is difficult to make conclusive statements as to which treatment age(s) produce(s) the largest increase. This in turn does not allow formulation of reliable forest management recommendations that are based on the model results alone. However, certain trends are visible in the results, which points out the usefulness of the model as a tool for testing of alternative management practices or hypotheses, and as an aid in making recommendations.

¹⁹Treatment at year 110 also showed maximum MAI at year 100. The reasons for this are discussed later.

As stated, the most substantial and continued increases in basal area of white spruce were produced by removal of trembling aspen at or before year 90. The magnitude of increase tends to diminish as treatment age increases. However, this is very susceptible to the influence of stochastic factors. In the later stages of the simulation runs, when most plots are at or near overmaturity, random death of the largest white spruce trees can have a prominent effect upon the amount of basal area present, and thus affect the maximum basal area attained. This would be the most probable reason as to why treatment at year 80 showed the largest maximum basal area. The plot treated at year 50 would likely have shown a larger maximum basal area if three separate runs had not exhibited extensive mortality of the largest-sized white spruce trees between years 110 and 120. The point at which maximum basal area of white spruce is attained is also very susceptible to influence by random mortality of large-sized trees. Therefore, there is no visible relationship between treatment age and the year in which maximum basal area occurs."

Stochastic factors caused the plot treated at year 70 to produce basal areas exceeding the control plot values before treatment occurred. Three simulation runs showed comparatively low frequencies of trembling aspen in the early stages of development, allowing white spruce to accumulate relatively high levels of basal area before treatment.

It appears that removal of trembling aspen at years 100 and 110 has little or no effect upon basal area accumulation of white spruce. The major reason is that at these treatment ages, many simulation runs have few or no aspen trees left to remove. In both cases, the slight increase in basal area of spruce over the control plot values between years 145 and 150 is probably due only to random mortality on the control plot. Even though basal areas for both treatment ages were consistently below those of the control plot before removal,²⁰ again due to the influence of stochastic factors, neither treatment age showed a visible increase in basal area accumulation after removal.

Stochastic elements likely play a major role in the decrease in year of maximum MAI between treatment at years 80 and 90. This would also be the main reason for the further decrease for treatment at years 100 and 110, as it is very probable that treatment at these ages has no effect upon basal area accumulation of white spruce. In fact, for treatment at year 110, maximum MAI occurs ten years before treatment.

The relationship between treatment age and year of maximum MAI should be viewed cautiously, as in some cases, MAI remains relatively constant for rather long periods of time. For example, the control plot shows a difference of 1.06 cm²/yr between the highest and lowest values recorded between years 90 and 130, and MAI at year 110 is 0.13 cm²/yr

²⁰The only exception is for years 92 to 104, when basal area for treatment at year 110 slightly exceeded the control plot basal area.

less than the maximum recorded at year 130. Treatment at year 70 shows a difference of $1.91 \text{ cm}^2/\text{yr}$ between the highest and lowest values recorded between years 100 and 130, and MAI at year 100 is only $0.01 \text{ cm}^2/\text{yr}$ less than the maximum recorded at year 130. Since basal area can be readily affected by the influence of stochastic factors, especially in later years, MAI, which is mathematically derived from basal area, is similarly affected.

The random variation within the results of this case study could be reduced by using the same set of pseudo-random starting points for all sets of treatment runs. This would cause average basal area values for each treatment age to be identical to those for the control plot until trembling aspen is removed. Increasing the number of runs per treatment age to, for example, 100 would also reduce the effects of stochastic factors within the model. However, to do so was definitely beyond the scope of this case study.

Data shortages also caused some problems in the reliability of the model predictions. As mentioned, a lack of conclusive data prevented inputting of artificial frequencies for white spruce for treatment at year 0. The completeness of the model frequencies would have been increased if treatment at years 10 and 20 could have been tested.

5. Implications for Trembling Aspen: It is interesting to observe how recovery of trembling aspen is influenced by the age at which it is completely removed from the stand. Table 12 shows recovery of average basal area of trembling aspen,

per age of removal. Maximum frequency and average frequency per age class are also indicated.

Trembling aspen showed highest recovery for removal at years 0 and 30. There is a rather prominent decrease in average basal area from removal at age 30 to removal at age 40. Average frequency per age class also shows a visible decrease. Subsequent to removal at year 40, the magnitude of recovery in basal area continues to decrease, but at a more gradual rate. Maximum frequency tends to show an overall decrease, and then levels out at three trees, while average frequency per age class shows an overall decrease. The only exception is for removal at 50 years, which shows higher basal area in some age classes than removal at 40 years. Maximum frequency and average frequency per age class are also slightly higher. These anomalies are likely the result of stochastic factors in the birth and mortality functions for trembling aspen, and are therefore of little consequence.

The trends noted above would be expected, since as age of removal increases, increasingly larger-sized white spruce trees will cast increasingly higher levels of shade. This lowers the probability of establishment of trembling aspen saplings, and increases the probability of suppression and mortality of any saplings that do establish. As well, there is a direct decrease in the amount of time available for trembling aspen to establish, and accumulate basal area.

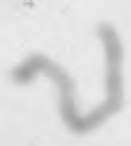


Table 12. Case study III: recovery of average basal area of trembling aspen after complete removal, by age of removal.

	AVERAGE BASAL AREA (cm ²)									
	0	30	40	50	60	70	80	90	100	110
10	5.5									
20	20.3									
30	24.1									
40	59.3	6.1								
50	99.2	30.6	3.2							
60	141.4	70.4	18.7	5.8						
70	174.0	142.3	38.7	25.9	2.5					
80	143.1	192.0	60.0	47.2	10.7	1.6				
90	163.4	240.5	80.0	58.3	16.3	8.2	0.9			
100	165.9	289.7	66.3	68.4	20.6	25.5	2.5	1.1		
110	129.7	310.5	67.0	77.5	23.1	20.0	5.9	5.3	0.2	
120	114.7	267.7	63.7	98.3	29.2	18.4	11.8	8.8	2.0	0.5
130	133.8	269.8	29.9	74.3	36.8	15.7	9.3	9.5	4.3	2.0
140	156.6	151.0	38.1	46.6	32.0	3.4	15.3	15.2	5.6	5.1
150	83.1	157.7	20.1	56.3	37.2	9.8	11.8	26.4	12.3	9.8
MAX. FREQ.	5	5	4	5	4	3	2	3	3	3
AVERAGE FREQ. PER AGE CLASS	1.9	1.6	1.1	1.2	0.8	0.6	0.7	0.5	0.5	0.3

VII. APPLICATION TO THEORY REGARDING MECHANISMS AND PROCESSES PRODUCING SPECIES SEQUENCES DURING SUCCESSION

The basic premise of the following discussion is that since the JABOR growth model successfully reproduces the development of upland white spruce-trembling aspen stands in the western Canadian boreal forest, the assumptions and mathematical relationships of the simulator should be accurate representations of the successional processes and mechanisms characteristic of such sites. Through comparison of the model assumptions and relationships to classical and contemporary successional theory, the model can aid in supporting or questioning current knowledge regarding the principles underlying species sequences.

As the JABOR model applies only to upland white spruce-trembling aspen sites, little can be said about succession in other boreal forest community types. Some conjectures or parallels may be drawn, however, as many studies indicate that, within the boreal ecosystem, communities and site types that are relatively similar tend to exhibit similar ecological and successional processes (Dix and Swan 1971; Corns and La Roi 1976; Carleton and Maycock 1978); Larsen 1980). Since JABOR deals only with tree species, the role of and importance of lesser and understory vegetation are given only cursory treatment. Finally, it should be pointed out that forest growth models very different in underlying assumptions and rationale from JABOR have produced highly accurate results for, among other

things, tree species sequences in the forest communities or ecosystems they are designed to simulate. Therefore, the scope of this discussion must be limited to providing observations and speculations that require further investigation or verification before being treated as conclusive.

In almost all of its assumptions and basic principles, the JABOR model supports contemporary successional theory. It is an individual tree-based growth model, and therefore considers the individual organism as the basic component of the forest community and the successional process. The model also strongly emphasizes life strategies, and the ecophysiological characteristics that define these strategies. Trembling aspen is defined as an opportunistic species that enters open sites rapidly and in relatively high numbers (birth function). It is faster-growing (G) than white spruce, and has a greater height per diameter at young to middle ages (growth function). However, it is shorter-lived (AGEMX), and shade intolerant (ITYPE and AINC), and therefore tends to carry out its life cycle relatively faster, and be less competitive at lower levels of resource availability. White spruce is defined as a conservative species that invades a stand in low numbers and grows slowly, but which can outlast the fast-growing and intolerant trembling aspen and eventually achieve a position of stand dominance. It can be seen that both types of species strategies can be effectively simulated through a

relatively small number of rather simple assumptions.

In order to produce predicted stands that matched the observed stands of the validation data, the assumption was made that after trembling aspen initially invades a site, in most cases, small numbers of aspen saplings will continue to establish through all stand ages. This assumption is corroborated by the observations of Larsen (1980), and the results of studies by Dix and Swan (1971). Therefore, the observation that intolerant or opportunistic species will often persist through all stages of succession, as put forth by contemporary theory, is supported. In later stages of succession on the simulation plots, the majority of trembling aspen saplings establish in response to stand opening caused by the death of one or more large white spruce individuals, which is in agreement with a mechanism of persistence proposed by Horn (1974) and Bormann and Likens (1979). Due to a lack of conclusive data for stands older than 200 years of age, the predictions of the model regarding the persistence of trembling aspen in such stands should be viewed as tentative.

Another assumption made in order to produce accurate model predictions was that white spruce established in most mixedwood stands within the first few years after disturbance. This assumption is supported by evidence from a wide range of forest types within the boreal forest (Dix and Swan 1971; Carleton and Maycock 1978; Larsen 1980). Therefore, the model predictions lend evidence that the

majority of species appearing in a sequence establish as succession starts or soon after (*sensu* contemporary theory).²¹ The functions and algorithms of JABOR do not indicate whether trembling aspen effects habitat modifications that facilitate the establishment and growth of white spruce, as would be expected according to classical theory. However, it would seem that through prolific establishment and rapid growth, trembling aspen "attempts" to monopolize growing space, light, and resources. By doing so, it decreases the probability of introduction of white spruce, and suppresses the growth of any spruce seedlings that do establish. This would constitute support of contemporary theory.

In a similar manner, the model simulates the mechanisms by which, according to contemporary theory, stages of dominance can be delayed or offset. For example, in a small number of simulation runs, growth of the initial white spruce crop is severely suppressed by a highly competitive trembling aspen component. In a number of other runs, white spruce enters the stand in very low numbers, which could imply inhibition of invasion and establishment of spruce by trembling aspen, or delays in immigration, for whatever reason. In both cases, the point at which white spruce attains stand dominance can be delayed considerably. Since the birth function for white spruce does not allow the

²¹The fact that trees are introduced at sapling size in JABOR does not affect this conclusion, nor the one drawn previously regarding persistence of intolerant or opportunistic species.

species to enter a site in relatively high numbers at any time, the model cannot be effectively used to simulate cases where spruce attains dominance significantly ahead of when it characteristically does so (*sensu* contemporary theory). This can be compensated for to an extent through interactive manipulation of initial white spruce frequencies, although a lack of pertinent data makes this difficult.

In general, the model effectively reproduces the structural changes which occur during succession that contribute to the suppression of trembling aspen, as per classical and contemporary theory. Increasing size of dominant trees causes increased levels of shading, adversely affecting the reproduction, growth ($R(AL)$ function), and chance of survival of the intolerant trembling aspen. This is especially the case for white spruce trees, which have a much greater weight of leaves per diameter (C and F) than aspen trees. Increased size of dominant trees also results in increased competition for space and resources ($S(BAR)$ function).

The stochastic nature of the JABOR model constitutes support of contemporary successional theory. The stochastic functions for introduction of white spruce and random addition of trembling aspen implicitly duplicate the stochastic factors that influence the plant-by-plant replacement process, such as availability of space, supply of propagules, and proximity of propagules to an opening. The stochastic nature of the function for introducing

trembling aspen to open sites contains, to a degree, implicit reproduction of the effects of supply of asexual and/or sexual propagules to the site, variations in environmental conditions, and type and degree of disturbance. The probabilistic nature of the mortality functions reproduces well the effects of the deaths of single trees, and implicitly, the causes and agents of death, upon the patterns of establishment, growth, and survival of individuals of both species.

As a result of the stochastic factors within the model, individual plots show wide variability in stand characteristics at a given point in time, and in timing of events (*sensu* contemporary theory). It has been demonstrated (page 87) that individual model runs show wide differences in basal area of white spruce at selected age classes. There are also wide ranges in values for basal area for trembling aspen, and for frequencies and diameter distributions of both species. It has been shown (page 77) that there is wide variability in the stand age at which trembling aspen initially disappears from the simulated plots.

As the JABOR model includes only two tree species, the species sequences that are produced tend to be highly unidirectional and predictable, as would be expected according to classical theory. However, this is only a relative observation, since in boreal communities, the number of possible successional stages and pathways increases directly with species diversity (Dix and Swan

1971; Carleton and Maycock 1978; Larsen 1980). This constitutes support for the principle, as put forth by contemporary theory, that in communities or ecosystems with relatively low species diversities, there is little amplitude for variability within the species sequences that occur.

The relatively low species diversity of the stands simulated by JABOR provides marginal support for another aspect of contemporary theory. Since white spruce establishes within the first few years on almost all simulation runs, and trembling aspen persists into the later stages of many, it would seem that succession is a process of shifting stages of dominance,²² and not one of continuous changes in species composition (*sensu* classical theory). Any appearance of orderly species replacement is an overt expression of species conspicuousness, which reflects differing life strategies.

The predictions of the JABOR model can be used to speculate upon the nature of the climax stage of succession in upland white spruce-trembling aspen forests. It is difficult to make a definite statement as to when the climax stage actually begins, but based on the predictions of the model for total plot basal area and biomass, the starting-point would be in the vicinity of year 210. This is the point at which the irregular oscillations in basal area

²²Dominance in this discussion refers to dominance of standing, living biomass. This involves size and height of organisms, and species abundance.

and biomass, as previously described, appear to begin. In a hypothetical old-age forest made up of a composite of all simulation runs, plots in all stages of maturity, break-down, and recovery are represented. Due to the presence of individual plots that are undergoing changes of varying magnitude, the ecosystem would not achieve a high degree of internal stability,²³ but in the absence of major disturbance, would exhibit a state of overall structural and functional stability, as per contemporary theory. The conservative life-strategy of white spruce ensures that it will maintain overall dominance, especially since no plots experienced sufficient opening to allow prolific invasion and dominance by trembling aspen. The nature of the simulated old-age stands casts doubt upon the observation that climax communities are characterized by high degrees of stability, as put forth by classical theory. In addition, due to the ubiquity and commonness of fire as an agent of disturbance in the boreal forest, the supposition of classical theory that climax communities are frequent and inevitable occurrences, with wide areal and temporal extent, must be questioned.

²³Stability is defined as the capacity of an ecosystem to persist in the presence of destructive or destabilizing forces (after Bormann and Likens 1979a).

VIII. SUMMARY AND CONCLUSIONS

The JABOR forest growth model successfully reproduces the growth and development of upland white spruce-trembling aspen stands in the western Canadian boreal forest. This includes accurate simulation of tree species succession, species frequencies, diameter distributions, and basal areas. The model can be used to predict above-ground living biomass, and predicts a peak standing crop for the forest at 120 years after disturbance, well before the climax stage of succession is reached. This supports the recent propositions of Bormann and Likens (1979a,b) concerning biomass accumulation in a forested ecosystem. In addition, the assumptions and mathematical relationships used in JABOR question conventional theory regarding the ecological processes that result in species sequences during succession, and lend support to many principles of contemporary theory.

Predictions of the JABOR model to 500 years show white spruce remaining as the dominant species in old-age stands, and trembling aspen present only as a minor constituent. These long-term predictions produce a climax forest that exhibits overall structural and functional stability, even though there is not a high degree of internal stability, as individual plots may be undergoing changes of varying magnitude. There are no validation data with which to conclusively verify the predictions of the model between years 200 and 500, and it is possible that the importance of

trembling aspen during all or part of this period is overestimated.

At present, the major uses of the JABOR growth model are in the testing of alternative forest management practices and hypotheses, and in analysing the responses of a forest to alternative ecological situations. A wide range of forest management-related topics can be investigated, with the greatest potential for use lying in studies of a silvicultural nature. In this project, the effects of varying environmental conditions upon tree growth and stand development were not explored. Consequently, the model could immediately be put to use in studying the effects of changes in temperature regime, as this parameter can be manipulated interactively.

The JABOR model is still in a developmental state, and there is much scope and opportunity for improvement. At present, improvement of simulation is limited mainly by a lack of relevant and readily available data for tree species in the western Canadian boreal forest, rather than the need for entirely new assumptions and mathematical relationships. Obtaining of sufficient data for validation of the model was a problem, especially for very young and very old stands. As pertinent data become available, it should be a relatively simple procedure to include more tree species in the model, and to widen the range of boreal communities and site types to which the model can be applied. The present version of the JABOR model, and future versions, can aid in pointing

out gaps in our information base on western Canadian boreal forests, and in determining priorities and objectives for future field research.

Literature Cited

- Alexander, M. E. and D. L. Euler. 1981. Ecological role of fire in the uncut boreal mixedwood forest. IN: Proceedings of the Boreal Mixedwood Symposium. Env. Can., Can. For. Serv., Great Lakes For. Res. Cent. COJFRC Symp. Proc. O-P-9. p. 42-64.
- Baskerville, G. L. 1965. Dry matter production in immature balsam fir stands. For. Sci. Monogr. 9:1-42.
- Bella, I. and J. P. DeFrancheschi. 1980. Biomass productivity of young aspen stands in western Canada. Env. Can., Can. For. Serv., Info. Rep. NOR-X-219. 23 p.
- Bormann, F. H. and M. F. Buell. 1964. Old-age stand of hemlock in central Vermont. Bull. Torrey Bot. Club 91:461-465.
- Bormann, F. H. and G. E. Likens. 1979a. Pattern and process in a forested ecosystem. Springer-Verlag, New York. 253 p.
- Bormann, F. H. and G. E. Likens. 1979b. Catastrophic disturbance and the steady state in northern hardwood forests. Amer. Sci., 67:660-669.
- Bormann, F. H., T. G. Siccama, G. E. Likens, and R. H. Whittaker. 1970. The Hubbard Brook ecosystem study: composition and dynamics of the tree stratum. Ecol. Monogr. 40:373-378.
- Botkin, D. B. 1974. A functional approach to the niche concept in forest communities. Sch. For. and Env. St., Yale University, New Haven. 38 p.
- Botkin, D. B., J. F. Janak, and J. R. Wallis. 1971. Some ecological consequences of a computer model of forest growth: Contr. No. 43, Hubbard Brook Ecosystem Study. Pre-publication manuscript. New York. 42 p.
- Botkin, D. B., J. F. Janak, and J. R. Wallis. 1972a. Rationale, limitations, and assumptions of a northeastern forest growth simulator. IBM J. Res. Development 16(2):101-116.
- Botkin, D. B., J. F. Janak, and J. R. Wallis. 1972b. Some ecological consequences of a computer model of forest growth. J. Ecol. 60:948-972.
- Braun, E. L. 1950. Deciduous forests of eastern North

- America. Blackiston Co., Philadelphia. 596 p.
- Brinkman, K. A. and E. J. Roe. 1975. Quaking aspen: silvics and management in the Lake States. USDA For. Serv. Agric. Handbook 486. 52 p.
- Brown, J. K. 1978. Weight and density of crowns of Rocky Mountain conifers. USDA For. Serv. Res. Pap. INT-197. 18 p.
- Buchman, R. G. and S. R. Shifley. 1983. Guide to evaluating forest growth projection systems. J. For. 81:232-234.
- Carleton, T. J. and P. F. Maycock. 1978. Dynamics of the boreal forest south of James Bay. Can. J. Bot. 56:1157-1173.
- Carleton, T. J. and P. F. Maycock. 1980. Vegetation of the boreal forest south of James Bay: non-centered component analysis of the vascular flora. Ecology 61:1199-1212.
- Clements, F. E. 1916. Plant succession. Carnegie Inst. Wash. Publ. 242. 512 p.
- Clements, F. E. 1920. Plant indicators. Carnegie Inst. Wash. Publ. 290. 338 p.
- Clements, F. E. 1928. Plant succession and indicators. H. W. Wilson, New York. 453 p.
- Colinvaux, P. A. 1973. Introduction to ecology. John Wiley and Son, New York. 621 p.
- Connell, J. H. 1972. Community interactions on marine rocky intertidal shores. Ann. Rev. of Ecol. Syst. 3:169-192.
- Connell, J. H. and R. O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. Amer. Nat. 111:1119-1144.
- Cooper, W. S. 1926. The fundamentals of vegetational change. Ecology 7:391-413.
- Corns, I. G. W. and G. H. La Roi. 1976. A comparison of mature with recently clear-cut and scarified lodgepole pine forests in the Lower Foothills of Alberta. Can. J. For. Res. 6:21-32.
- Cowles, H. C. 1899. The ecological relations of the vegetation of the sand dunes of Lake Michigan. Bot. Gaz. 27:95-117, 167-202, 281-308, 361-391.
- Cowles, H. C. 1901. The physiographic ecology of Chicago and

- vicinity. Bot. Gaz. 31:73-108, 145-182.
- Dansereau, P. 1957. Biogeography - an ecological perspective. Ronald Press Co., New York. 392 p.
- Daubenmire, R. 1968. Plant communities. Harper and Row, New York. 392 p.
- Davis, R. B. 1966. Spruce-fir forests of the coast of Maine. Ecol. Monogr. 36:79-94.
- Day, R. J. and E. M. Harvey. 1981. Forest dynamics in the boreal mixedwood. IN: Proceedings of the boreal mixedwood symposium. Env. Can., Can. For. Serv., Great Lakes For. Res. Cent. COJFRC Symp. Proc. O-P-9. p. 29-41.
- Dempster, W. R. and Associates. 1983. Forestry research needs for the management of aspen and poplar in Alberta. Unpublished report prepared for the Alberta Forest Service. 54 p.
- Dix, R. J. and J. M. A. Swan. 1971. The roles of disturbance and succession in upland forests at Candle Lake, Saskatchewan. Can. J. Bot. 49:657-676.
- Doucet, R., J. Berglund, and C. Farnsworth. 1976. Dry matter production in 40-year old *Pinus banksiana* stands in Quebec. Can. J. For. Res. 6:357-367.
- Doyle, I. W. 1981. The role of disturbance in the gap dynamics of a montane rain forest. IN: Forest succession: concepts and applications. West, D. C., H. H. Shugart, and D. B. Botkin (eds.). Springer-Verlag, New York. p. 56-73.
- Drury, W. H. and I. C. T. Nisbet. 1973. Succession. J. Arnold Arboretum 54:331-368.
- Egler, F. E. 1954. Vegetation science concepts: I. Initial floristic composition - a factor in old-field vegetation development. Vegetatio 4:412-417.
- Ek, A. R. 1974. Nonlinear models for stand table projection in northern hardwood stands. Can. J. For. Res. 4:23-27.
- Ek, A. R. and A. Dudek. 1980a. A bibliography of worldwide literature on individual tree-based forest stand growth models. Coll. For., Univ. Minnesota, St. Paul. Staff Pap. 12. 33 p.
- Ek, A. R. and A. Dudek. 1980b. Development of individual tree-based stand growth simulators: progress and applications. Coll. For., Univ. Minn., St. Paul. Staff

Pap. 20. 25 p.

- EK, A. R. and R. A. Monserud. 1974a. FOREST: a computer model for simulating the growth and reproduction of mixed forest stands. Coll. Agric. Life Sci., Univ. Wisconsin, Madison. Res. Rep. A2635. 14 p.
- EK, A. R. and R. A. Monserud. 1974b. Trials with program FOREST: growth and reproduction simulation for mixed-species even or uneven-aged forest stands. IN: Growth models for tree and stand simulation. Fries, J. (ed.). Royal College For., Stockholm. Res. Note 30. p. 56-73.
- Energy, Mines, and Natural Resources. 1970. National atlas of Canada. Printed by Surveys and Mapping Branch, Ottawa, Ontario. 254 p.
- Energy, Mines, and Natural Resources. 1978. Hydrologic atlas of Canada. Printed by Surveys and Mapping Branch, Ottawa, Ontario. 34 plates.
- Environment Canada. 1982. Canadian climate normals, temperature and precipitation: 1951-1980. Vol. 3. Compiled by Atmospheric Environment Service, Downsview, Ontario. 429 p.
- Fowells, H. A. (ed.). 1965. Silvics of forest trees of the United States. USDA For. Serv. Agric. Handbook 271. 762 p.
- Freedman, B., P. N. Duinker, H. Barclay, R. Morash, and U. Prager. 1982. Forest biomass and nutrient studies in central Nova Scotia. Env. Can., Can. For. Serv., Info. Rep. M-X-134. 126 p.
- Gleason, H. A. 1926. The individualistic concept of the plant association. Bull. Torrey Bot. Club 53:7-26.
- Goodall, D. W. 1972. Building and testing ecosystem models. IN: Mathematical models in ecology. Jeffers, J. N. R. (ed.). Blackwell Scientific Publications, Oxford. p. 173-194.
- Grabowski, T. I. J. 1981. A stand growth model for trembling aspen in the prairie provinces of Canada. M. Sc. thesis, Dept. For. Sci., Univ. Alberta, Edmonton, Alberta. 125 p.
- Harlow, W. M. and E. S. Harrar. 1941. Textbook of dendrology. McGraw-Hill, New York. 542 p.
- Hegy, F. 1972. Dry matter production in jack pine stands in Ontario. For. Chron. 481:1-5.

- Hegyi, F. 1974. A simulation model for managing jack pine stands. IN: Growth models for tree and stand simulation. Fries, J. (ed.). Royal College For., Stockholm. Res. Note. 30. p. 74-87.
- Heinselman, M. L. 1963. Forest sites, bog processes, and peatland types in the Glacial Lake Agassiz Region, Minnesota. Ecol. Monogr. 33:327-374.
- Heinselman, M. L. 1970. Landscape evolution, peatland types, and the environment in the Lake Agassiz Peatlands Natural Area, Minnesota. Ecol. Monogr. 40:235-261.
- Holdaway, M. R. and G. J. Brand. 1981. An evaluation of the STEMS tree growth projection system. Pre-publication manuscript. USDA For. Serv., North Cent. For. Exp. Stn., St. Paul, Minn. 43 p.
- Horn, H. S. 1974. The ecology of secondary succession. Ann. Rev. of Ecol. Syst. 5:25-37.
- Horn, H. S. 1975. Forest succession. Sci. Am. 232:90-98.
- Hosie, R. C. 1973. Native trees of Canada. Env. Can., Can. For. Serv., Ottawa, Ont. Seventh Ed. 380 p.
- Hutchinson, G. E. 1957. Concluding remarks, Cold Spring Harbor Symposium. Quant. Biol. 22:415-427.
- Hutchinson, G. E. 1965. The ecological theater and the evolutionary play. Yale University Press, New Haven. 139 p.
- Jarvis, J. M., J. C. Lees, R. M. Waldron, and G. A. Steneker. 1966. Review of silvicultural research; white spruce and trembling aspen types; mixed-wood forest section; boreal forest region; Alberta-Saskatchewan-Manitoba. Dept. For. Rur. Dev., For. Br. Dept. Publ. 1156. 189 p.
- Johnson, W. C. and D. M. Sharpe. 1976. An analysis of forest dynamics in the Northern Georgia Piedmont. For. Sci. 22:307-322.
- Johnstone, W. D. 1977. Interim equations and tables for the yield of fully-stocked spruce-poplar stands in the mixedwood forest section of Alberta. Env. Can., Can. For. Serv., Info Rep. NOR-X-175. 23 p.
- Kelsall, J. P., E. S. Telfer, and T. D. Wright. 1977. The effects of fire on the ecology of the boreal forest with particular reference to the Canadian north: a review and selected bibliography. Env. Can., Can. Wild. Serv.,

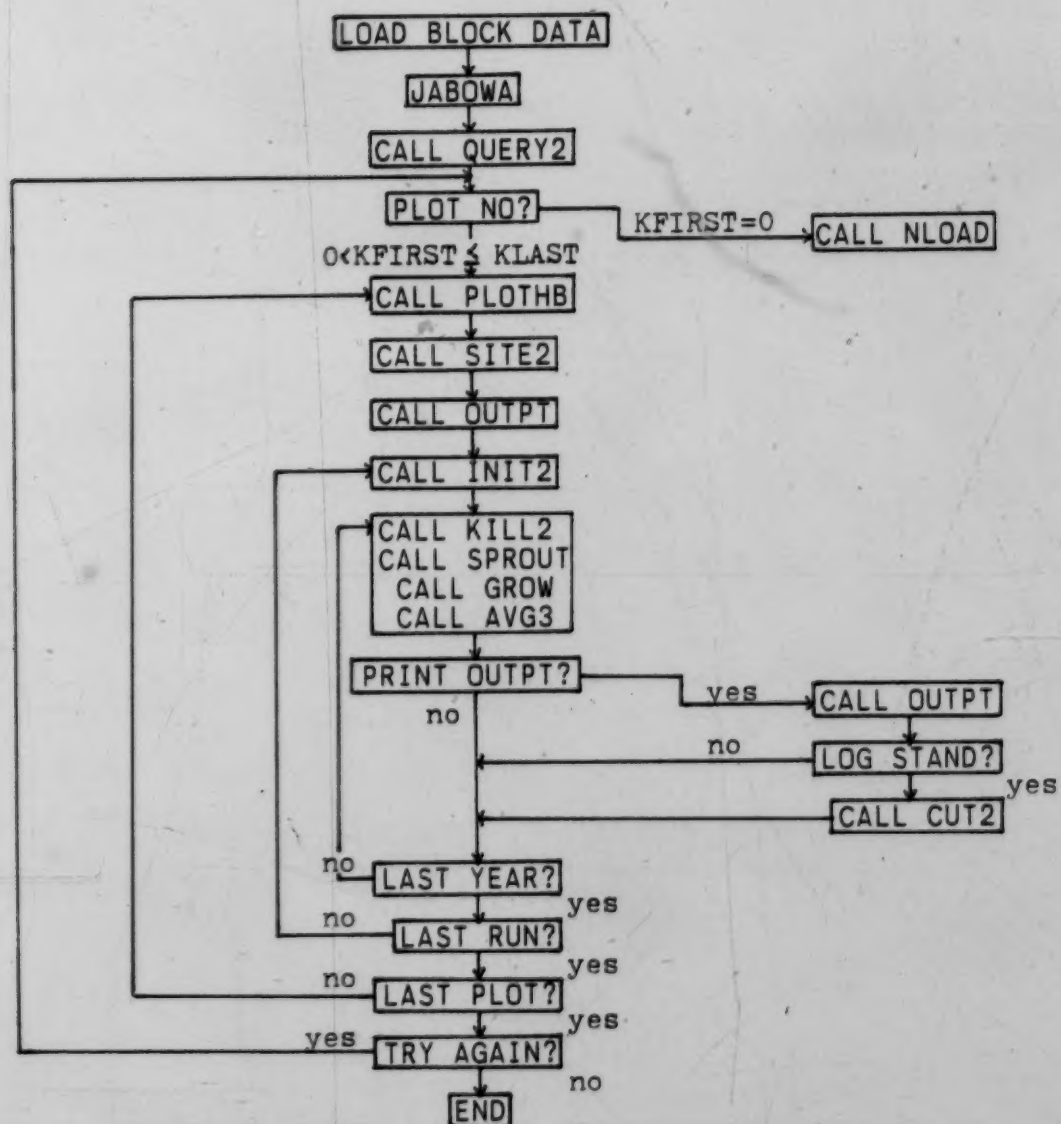
Ottawa, Ontario. Occas. Pap. 32. 57 p.

- Kirby, C. L., W. S. Bailey, and J. C. Gilmour. 1957. The growth and yield of aspen in Saskatchewan. Sask. Dept. Nat. Res., For. Br., Tech. Bull. 3. 67 p.
- Larsen, J. A. 1980. The boreal ecosystem. Academic Press, Toronto. 500 pp.
- Leak, W. B. 1970. Successional change in northern hardwoods predicted by birth and death simulation. Ecology 51:794-801.
- Lees, J. C. 1966. Release of white spruce from aspen competition in Alberta's spruce-aspen forest. Can. Dept. For. Publ. 116. 16 p.
- Levins, R. 1968. Evolution in changing environments. Princeton University Press, Princeton, N. J. 120 p.
- Loucks, O. L. 1970. Evolution of diversity, efficiency, and community stability. Amer. Zool. 10:17-25.
- MacArthur, R. H. 1972. Geographical ecology. Harper and Row, New York. 269 p.
- Marquis, D. A. 1967. Clear-cutting in northern hardwoods. USDA For. Serv. Res. Pap. NE-85. 13 p.
- McCormick, J. 1968. Succession. IN: VIA 1, Student Publication, Graduate School of Fine Arts, Univ. Pennsylvania, Philadelphia. p. 22-35, 131, 132.
- Mielke, D. L., H. H. Shugart, and D. C. West. 1978. A stand model for upland forests of southern Arkansas. Oak Ridge National Laboratory, Oak Ridge. ORNL HM-6225. 21 p.
- Mitchell, K. J. 1975. Dynamics and simulated yield of Douglas fir. For. Sci. Monogr. 17:1-39.
- Moser, J. W. 1972. Dynamics of an uneven-aged forest stand. For. Sci. 18:184-191.
- Munro, D. 1974. Forest growth models - a prognosis. IN: Growth models for tree and stand simulation. Fries, J. (ed.). Royal College For., Stockholm. Res. Note 30. p. 7-21.
- Neiring, W. A. and F. E. Egler. 1955. A shrub community of *Viburnum lentage*, stable for twenty-five years. Ecology 36:356-360.
- Neiring, W. A. and B. H. Goodwin. 1974. Creation of relatively stable shrublands with herbicides: arresting

- succession on rights-of-way and pastureland. *Ecology* 55:784-795.
- Nichols, G. E. 1923. A working basis for the ecological classification of plant communities. *Ecology* 4:11-23, 154-172.
- Odum, E. P. 1959. *Fundamentals of ecology*. W. B. Saunders and Co., Philadelphia. 546 p.
- Odum, E. P. 1971. *Fundamentals of ecology*. W. B. Saunders and Co., Philadelphia. Third ed. 574 p.
- Peterson, E. B., Y. H. Chan, and J. J. Cragg. 1970. Above-ground standing crop, leaf area, and caloric value in an aspen clone near Calgary, Alberta. *Can. J. Bot.* 48:1459-1469.
- Phipps, R. L. 1979. Simulation of wetland forest vegetation dynamics. *Ecol. Modeling* 7:257-288.
- Reed, K. J. 1980. An ecological approach to modelling growth of forest trees. *BioScience* 26:33-50.
- Rowe, J. S. 1972. Forest regions of Canada. *Env. Can., Can. For. Serv., Publ.* 1300. 172 p.
- Schaeffer, D. L. 1980. A model evaluation methodology applicable to environmental assessment models. *Ecol. Modeling* 8:275-295.
- Shugart, H. H., M. S. Hopkins, I. R. Burgess, and A. T. Mortlock. 1981. The development of a succession model for a subtropical rain forest and its application to assess the effects of timber harvest at Wiangree State Forest, New South Wales. *J. Env. Mgt.* 11:243-265.
- Shugart, H. H., S. B. McLaughlin, and D. C. West. 1980. Forest models: their development and potential applications for air pollution effects research. *USDA For. Serv. Gen. Tech. Rep.* PSW-43. 14 p.
- Shugart, H. H. and I. R. Noble. 1981. A computer model of succession and fire response of the high altitude *Eucalyptus* forests of the Brindabella Range, Australian Capitol Territory. *Austr. J. Ecol.* 6:149-164.
- Shugart, H. H. and D. C. West. 1977. Development of an Appalachian deciduous forest succession model and its application to assessment of the impact of the chestnut blight. *J. Env. Mgt.* 5:161-179.
- Shugart, H. H. and D. C. West. 1980. Forest succession models. *BioScience* 5:308-313.

- Shugart, H. H. and D. C. West. 1981. Long-term dynamics of forest ecosystems. *Amer. Sci.* 69:647-652.
- Singh, T. 1982. Biomass equations for ten major tree species of the prairie provinces. *Env. Can., Can. For. Serv., Info. Rep. NOR-X-242.* 35 p.
- Sprugel, D. G. 1976. Dynamic structure of wave-generated *Abies balsamea* forests in the northeastern United States. *J. Ecol.* 64:889-911.
- Spurr, S. H. and B. V. Barnes. 1980. Forest ecology. John Wiley and Sons, Toronto.. Third edition. 686 p.
- Stearns, T. S. 1949. Ninety years of change in a northern hardwood forest in Wisconsin. *Ecology* 30:350-358.
- Steneker, G. A. 1974. Selective cutting to release white spruce in 75 to 100-year old white spruce-trembling aspen stands in Saskatchewan. *Env. Can., Can. For. Serv., Info. Rep. NOR-X-121.* 13 p.
- Sutton, R. F. 1969. Silvics of white spruce (*Picea glauca* (Moench) Voss). *Dept. Fish. For. - Can. For. Br. Publ.* 1250. 57 p.
- Tharp, M. L. 1978. Modelling major perturbations on a forest ecosystem. M. Sc. thesis, Univ. of Tennessee, Knoxville. 52 p.
- United States Department of Commerce. 1968. Climatic atlas of the United States. Govt. Printing Off., Washington, D. C. 124 p.
- Walker, D. 1970. Direction and rate in some British postglacial hydrosere. IN: The vegetational history of the British Isles. Walker, D. and R. West (eds.) Cambridge Univ. Press, Cambridge. p. 117-139.
- Watt, A. S. 1947. Pattern and process in the plant community. *J. Ecol.* 35:889-911.
- Westman, W. E. 1968. Invasion of fir forest by sugar maple in Itasca Park, Minnesota. *Bull. Torrey Bot. Club* 95:172-186.
- Whittaker, R. H. 1975. Communities and ecosystems. MacMillan, New York. Second ed. 385 p.
- Whittaker, R. H., F. H. Bormann, G. E. Likens, and T. G. Siccama. 1974. The Hubbard Brook Ecosystem study: forest biomass and production. *Ecol. Monogr.* 44:233-254.

**IX. APPENDIX I: FLOW CHART FOR JABOWA (VERSION II) AND
GENERAL SUMMARY OF PROGRAM BY SUBROUTINE**



Flow chart for JABOWA (Version II), from Botkin et al. (1972a).

General Summary Of Program

1. BLOCK DATA: provides data
2. JABOWA: the main program
3. QUERY2: displays parameters, with default values, and program information that can be interactively altered by the user.
4. NLOAD: tree data for the plot, derived from a dummy sample plot, which may be used to start the run.
5. PLOTHB: supplies actual plot data, and can be used instead of NLOAD.
6. SITE2: provides estimates of site quality, based on growing-degree days and an estimate of evapotranspiration.
7. OUTPT: prints the zero-year stand, and then current plot information at user-specified intervals. Print-out includes: year of run, species present, number of trees per species, diameter at breast height (DBH) per tree, basal area (BA) per species, plot leaf area, and biomass values for the plot, per tree component. If desired by the user, it can display calculation of averages of DBH and BA since the last print-out, information on dead trees, or call subroutine CUT2.
8. CUT2: all trees larger than a user-specified diameter can be removed from the plot, to simulate disturbance. The species can also be logged differentially.
9. INIT2: when doing more than one run for a plot, returns the plot to zero-year conditions.
10. KILL2: trees are removed from the plot, by one of two separate mechanisms:
 - a. age-independent;
 - b. growth-dependent; reflects suppression.Also updates lists of live and dead trees.
11. SPROUT: introduces new saplings to the plot.
12. GROW2: grows the remaining trees on the plot, using the species-specific growth rate equation.
13. AVG3: calculates totals and averages of numbers of trees and basal areas, for use in the output.

**X. APPENDIX II: SOURCE LISTING FOR JAVOR, SAMPLE RUN, AND
INDEX OF PARAMETERS THAT CAN BE CHANGED INTERACTIVELY**

Source Listing for JABOR

```

1 C JABOR - A GROWTH SIMULATOR FOR UPLAND WHITE SPRUCE-TREMBLING
2 C ASPEN STANDS IN ALBERTA
3 C
4 C THIS PROGRAM IS A MODIFICATION OF JABOWA, VERSION II
5 C (BOTKIN ET AL. 1971, 1972a,b)
6 C
7 DIMENSION DBH(500), NTREES(5)
8 DIMENSION DBH(500), NTREES(5)
9 COMMON /DATA/ G(5), ITYPE(5), AGEMX(5), C(5), F(5)
10 COMMON /RUNNR/ NYR, I, KPNT, KAGE, KTIMES, KFIRST, KLAST
11 COMMON /TRACE/ IGES(500), IDGE(500)
12 COMMON /NDATA/ B2(5), B3(5), PHI, SOILO, DEGD, D
13 COMMON /CLIMAT/ DMIN(5), DMAX(5), BASEP(12), BASEF(12), BASEH
14 COMMON /PLOT/ IELEV, IROCK, TILL, SOILM, TEXT, EXCESS
15 COMMON /BIRTHK/ ASPWT, WMIN(5), WMAX(5)
16 COMMON /KILD/ NOGRO(500), ODBH(500), KDEAD(5), AREA, KD
17 COMMON /KILLR/ LOG, ALIMIT(5)
18 COMMON /AVER/ ATR(5), ASR(5), YTR, TBR, IAYER
19 COMMON /OUTCON/ NODBH
20 COMMON /BIRSP/ NSPP
21 COMMON /SAPLG/ SAPNU(5)
22 COMMON /PHOTO/ A1, A2, A3
23 COMMON /SPEC/ AINC(5), BINC
24 DATA JYES/ 1N/
25 NAMELIST /NIQ/ KFIRST, KLAST, KTIMES, KPNT, KAGE, NYR, NODBH, IAYER
26 NAMELIST /NPT/ IELEV, IROCK, IX, TILL, TEXT, LOG, NTREES, DBH, PHI,
27 ISOIL, G, C, F, D, ITYPE, AGEMX, B2, B3, NSPP, SAPNU, AINC, A1, A2, A3, DMIN, DMAX, JABO0670
28 2, ALIMIT, ASPWT, WMIN, WMAX
29 NAMELIST /NR/ KPNT, LOG, KAGE, DBH, NTREES, G, C, F, D, ITYPE, AGEMX, B2, B3, PHI, JABO1040
30 I, SAPNU, AINC, A1, A2, A3, DEGD, DMIN, DMAX, WMIN, WMAX, NODBH, IAYER, ASPWT, AL, JABO1080
31 2, IMIT
32 III=1
33 IX=987843
34 DO 14 J=1,5
35 ALIMIT(J)= -11.0
36 KDEAD(J)=0
37 NODBH=0
38 CALL QUERY2 (DBH, NTREES)
39 DO 50 KK=1,5
40 NTREES(KK)=0
41 DO 51 KK=1,500
42 DBH(KK)=0.0
43 WRITE(6,21)
44 21 FORMAT(5X, '1/5 CHANGES? Y OR N?')
45 READ(5,22) KTEST
46 22 FORMAT(A1)
47 IF (KTEST.NE. JYES) GO TO 100
48 WRITE(6,23)
49 23 FORMAT(5X, 'ENTER ANID CHANGES=KFIRST, KLAST, KTIMES, KPNT, KAGE, NYR, NO, JABO0480
50 I, DBH, IAYER')
51 READ(5, NID)
52 CONTINUE
53 IPLOT=KFIRST
54 KSTART=KFIRST
55 IF (KFIRST .LT. 1 .OR. KFIRST .GT. 208) GO TO 7
56 DO 8 J=1, KSTART
57 CALL PLOTNR(IELEV, NUSED, NUSED, IROCK, NUSED, NUSED, NUSED, NUSED,
58 I, IPLOT, NTREES, DBH, KKSA, KSAPS, KKSE, KSEEDS, NOGRO, TILL)
59 CONTINUE
60 GO TO 10

```

```

61 C 7 CALL NLOAD(DBH, NTREES)
62 CONTINUE
63 WRITE(6,25)
64 25 FORMAT(5X, 'PLOT CHANGES? Y OR N?')
65 READ(5,22) KTEST
66 IF (KTEST.NE. JYES) GO TO 913
67 WRITE(6,27)
68 27 FORMAT(5X, 'ENTER ANPT CHANGES IN IELEV, IROCK, IX, TILL, TEXT, DMIN, DMAX, JABO0700
69 I, WMIN, WMAX')
70 WRITE(6,28)
71 28 FORMAT(5X, 'ASPWT, ALIMIT, LOG, NTREES, DBH, PHI, SOILO, ITYPE, AGEMX, B2, B3, JABO0730
72 I, NSPP,')
73 WRITE(6,29)
74 29 FORMAT(5X, 'SAPNU, AINC, A1, A2, A3, C, D, F, G')
75 READ(5, NPT)
76 913 CONTINUE
77 CALL SITE2
78 KSTART=FLOAT(IELEV)/3.2808*0.5
79 WRITE(6,13) IX
80 WRITE(6,12) IPLOT, IELEV, TILL, IROCK, DEGD, SOILM
81 13 FORMAT(3X, 'ELEVATION', 3X, 'SOIL', 3X, 'PERCENT', 3X, 'GROW', JABO0880
82 12 FORMAT(3X, 'PLOT', 3X, 'NUMBER', 3X, 'METERS', 3X, 'DEPTH', 3X, 'ROCK', JABO0880
83 11 INC, 3X, 'INDEX OF', 3X, 'ACTUAL ET', 3X, 'P10.1, P10.1, P10.1, P14.1)
84 11 INC, 3X, 'ACTUAL ET', 3X, 'P10.1, P10.1, P10.1, P14.1)
85 I=0
86 CALL OUTPT(DBH, NTREES)
87 CONTINUE
88 DO 9 JJ=1, KTIMES
89 IF (JJ .GT. 1) WRITE(6,13) IX
90 CALL INIT2(DBH, NTREES, DBH, NTREES, JJ)
91 DO 10 I=1, NYR
92 CALL KILL2(DBH, NTREES, IX)
93 CALL SPRGUT(IX, NTREES, DBH)
94 CALL GROW2(DBH, NTREES)
95 CALL AVER2(DBH, NTREES)
96 IF (I-KPNT=(1/KPNT).NE.0) GO TO 1
97 CALL OUTPT(DBH, NTREES)
98 111 WRITE(6,101)
99 READ(5,22) KTEST
100 IF (KTEST.NE. JYES) GO TO 1
101 IF (.NOT. (III.EQ.1)) GO TO 105
102 WRITE(6,102)
103 102 WRITE(6,103)
104 101 FORMAT(5X, 'CHANGES? Y OR N?')
105 III=2
106 102 FORMAT(10X, 'ENTER ANR CHANGES IN KPNT, KAGE, LOG, DBH, NTREES,')
107 103 FORMAT(10X, 'ITYPE, AGEMX, B2, B3, PHI, SAPNU, AINC, A1, A2, A3', 10X, 'DMIN, D, JABO1180
108 I, MAX, DEGD, WMIN, WMAX, NODBH, ASPWT, ALIMIT, G, C, F, D')
109 105 WRITE(6,979)
110 979 FORMAT(5X, 'ENTER ANR CHANGES')
111 READ(5, NR)
112 CONTINUE
113 9 CONTINUE
114 98 CONTINUE
115 IF (KFIRST .LT. 1) GO TO 99
116 IF (IPLOT .EQ. KLAST) GO TO 99
117 KSTART=1
118 SOILO=SOILO/(100.0-FLOAT(IROCK))/100.0)
119 GO TO 11
120 99 CONTINUE

```

```

121 WRITE(6,200)
122 200 FORMAT(IX,'WANT TO TRY AGAIN?')
123 READ(5,22)KTEST
124 IF(KTEST.EQ.JYES)GO TO 19
125 STOP
126 END
127 C -----
128 SUBROUTINE CUT2(DBH,NTREES)
129 DIMENSION DBH(500),NTREES(5),ANEW(500),KAGES(500)
130 COMMON/TRACE/ICES(500),IDCE(500)
131 COMMON/RUNNR/NYR,KYR,KPNT,KAGE,KTIMES,KFIRST,KLAST
132 COMMON/KILLR/LOG,ALIMIT(5)
133 NTOT=0
134 DO 1 I=1,5
135 NTOT=NTOT+NTREES(I)
136 CONTINUE
137 IF(NTOT.EQ.0) RETURN
138 DO 3 I=1,5
139 IF(ALIMIT(I).GT.0.0)GO TO 3
140 ALIMIT(I)=LOG
141 CONTINUE
142 LOG=-1
143 WRITE(6,14) (J,J=1,5), (ALIMIT(J),J=1,5)
144 14 FORMAT(10X/10X,'DIAMETER LIMITS FOR LOGGING BY SPECIES'/10X,515
145 +/10X,SPS.1/10X)
146 NEW=0
147 KBEG=1
148 KEND=0
149 DO 2 J=1,5
150 IF (NTREES(J).EQ.0) GO TO 2
151 KEND=NTREES(J)+KEND
152 DO 5 JJ=KBEG,KEND
153 J=JJ
154 IF (DBH(J).LT. ALIMIT(I)) GO TO 6
155 NTREES(I)=NTREES(I) -1
156 GO TO 5
157 5 NEW=NEW+1
158 ANEW(NEW)=DBH(J)
159 KAGES(NEW)=ICES(J)
160 CONTINUE
161 KBEG=KEND+1
162 CONTINUE
163 DO 13 KK=1,5
164 ALIMIT(KK)= -1
165 IF (NEW.EQ.0) GO TO 10
166 DO 7 I=1,NEW
167 DBH(I)=ANEW(I)
168 ICES(I)=KAGES(I)
169 CONTINUE
170 RETURN
171 10 CONTINUE
172 WRITE(6,11)
173 11 FORMAT(10X/10X,'ALL TREES WERE CUT'/)
174 DO 12 J=1,500
175 DBH(J)=0.0
176 ICES(J)=0
177 CONTINUE
178 RETURN
179 END
180 C -----

```

```

181 SUBROUTINE SPKDUY(IX,NTREES,DBH)
182 DIMENSION NTREES(5),ANEW(500),DBH(500),KAGE(500)
183 DIMENSION NEW(5)
184 COMMON/TRACE/ICES(500),IDCE(500)
185 COMMON /YDATA/E(5),ITYPE(5),ACEMX(5),C(5),F(5)
186 COMMON/KILD/NGRO(500),DDBH(500),KDEAD(5),AREA,KD
187 COMMON /BIRTHK/ASPWT,WMIN(5),WMAX(5)
188 COMMON /CLIMAT/DMIN(5),DMAX(5),BASEP(12),BASEP(12),BASEH
189 COMMON /HDATA/H2(5),H3(5),PHI,SOIL,DECD,D
190 COMMON /PLOTG/ISLEV,IRCK,TILL,SOILM,TEXT,EXCESS
191 COMMON /RUNNR/NYR,KYR,KPNT,KAGE,KTIMES,KFIRST,KLAST
192 COMMON/BIRSP/NSPP
193 COMMON/SAPLG/SAPNU(5)
194 SIZE=0.5
195 KW=1
196 KM=1
197 210 WEIGHT=0.0
198 NU=1
199 DO 230 LL=1,NSPP
200 L=LL
201 IF(NTREES(L).EQ.0) GO TO 230
202 NNU=NU+NTREES(L)-1
203 DO 220 MM=NU,NNU
204 M=MM
205 WEIGHT=WEIGHT+C(L)*DBH(M)*F(L)
206 NNU=NU+NTREES(L)
207 C WRITE(6,26)WEIGHT
208 26 FORMAT(IX,F10.3)
209 KEND=NU-1
210 IF(SOILM.LT. WMIN(2).OR. SOILM.GT. WMAX(2).OR. DECD.LT.
211 +DMIN(2))GO TO 74
212 IF(DECD.GT. DMAX(2))GO TO 78
213 DO 2 J=1,KEND
214 KAGE(J)=ICES(J)
215 ANEW(J)=DBH(J)
216 CONTINUE
217 N=2
218 CALL RANDOM(IX,R)
219 IF(WEIGHT.GT. 1.5E4)GO TO 20
220 IF(R.LT. 0.250)GO TO 78
221 GO TO 21
222 IF(WEIGHT.GT. 8.5E3)GO TO 21
223 IF(R.LT. 0.450)GO TO 78
224 GO TO 22
225 IF(R.LT. 0.515)GO TO 78
226 CALL RANDOM(IX,R)
227 R1 = R
228 M = SAPNU(2)+R1
229 IF(M.EQ.0) GO TO 78
230 KSUM=0
231 DO 51 I=1,M
232 KSUM=KSUM+NTREES(I)
233 DO 70 J=1,M
234 KSUM=KSUM+1
235 NTREES(N)=NTREES(N)+1
236 KAGE(KSUM)=0
237 CALL RANDOM(IX,R)
238 AZ=R-0.5
239 ANEW(KSUM)=SIZE+AZ
240 70 KEND=KEND+1

```



```

241 KIRKSUM=1
242 DO 50 I=K1,KEND
243 I=I+1
244 ANEW(I)=DBH(I-1)
245 NAGE(I)=ICES(I-1)
246 CONTINUE
247 IF(KEND.LT.50) GO TO 51
248 WRITE(9,98)
249 STOP
250 CONTINUE
251 98 FORMAT(' THE NTREES VECTOR IS TOO BIG',1314,' TRY COMPATIBLE SPEC
252 'IES AND CLIMATE')
253 DO 55 I=1,KEND
254 ICES(I)=NAGE(I)
255 DBH(I)=ANEW(I)
256 CONTINUE
257 IF(KN.GT.1) GO TO 74
258 IF(DEGD.GT.0) GO TO 74
259 N=1
260 IF(WEIGHT.GT.0) GO TO 18
261 CALL RANDOM(IX,R)
262 MADD=FIX(3.5*(R-0.5))
263 N=N+MADD
264 KN=KN+1
265 GO TO 50
266 18 CALL RANDOM(IX,R)
267 IF(WEIGHT.GT.1.784) GO TO 19
268 IF(R.LT.0.830) GO TO 74
269 GO TO 25
270 19 IF(WEIGHT.GT.3.0E4) GO TO 23
271 IF(R.LT.0.828) GO TO 74
272 GO TO 25
273 23 IF(R.LT.0.970) GO TO 74
274 25 CALL RANDOM(IX,R)
275 M=SAPNU(I)*R
276 IF(M.EQ.0) GO TO 74
277 KN=KN+1
278 GO TO 50
279 CONTINUE
280 75 DO 100 I=1,KEND
281 ICES(I)=ICES(I)+1
282 CONTINUE
283 RETURN
284 END
285 C
286 SUBROUTINE SITE2
287 DIMENSION SITET(12),PP(12)
288 COMMON /PLOTQ/IELEV,TROCK,TILL,SOILM,TEXT,EXCESS
289 COMMON /CLIMAT/ DMIN(5),DMAX(5),BASEP(12),BASEP(12),BASEH
290 COMMON /HDATA/S2(5),S3(5),PHI,SOILO,DEGD,K
291 ROCKY=(100.0-FLGAT(TROCK))/100.0
292 KPEL=IELEV/3.2808
293 SOILO=SOILO+ROCKY
294 DIFF=BASEH-FLGAT(KPEL)
295 TMIN=BASEP(1)+(2.2*DIFF/1000.0)
296 TMAX=BASEP(7)+(3.8*DIFF/1000.0)
297 TAVE=(TMAX+TMIN)/2.0
298 T=42.0
299 DEGD=(365.0/(2.0*3.14159))*((TMAX-TMIN)-(365.0/2.0)*(T-TAVE)
300 *+(365.0/3.14159)*(T-TAVE)/(TMAX-TMIN))

```

JAB02900
JAB02910
JAB02920
JAB02930
JAB02940
JAB02950
JAB02960
JAB02970
JAB02980
JAB02990
JAB03010
JAB03020
JAB03040
JAB03050
JAB03060
JAB03070
JAB03080
JAB03150
JAB03160

```

301 HEAT1 = 0.0
302 SOILM = 0.0
303 DO 10 I=1,12
304 SITET(I)=BASEP(I) + (3.8*DIFF/1000.0)
305 SITET(I)=(S.O/S.O)*(SITET(I) - 32.0)
306 PP(I)=BASEP(I)+28.4
307 IF(SITET(I).LE.0.0) GO TO 10
308 HEAT1 = HEAT1 + (SITET(I)/5.0)*1.514
309 CONTINUE
310 A = (0.875*(HEAT1+3.0) - 77.1*HEAT1+HEAT1 + 17930*HEAT1 + 4923
311 *50)/0.000001
312 N=1
313 STRMAX=AMIN1(TILL,10.0)*TEXT*ROCKY
314 DO 250 I=1,12
315 IF(SITET(I).LE.0.0) GO TO 250
316 PE = 18.0*((10.0*SITET(I)/HEAT1)+A)
317 IF(M.GT.1) GO TO 220
318 STOR=STRMAX
319 N=N+1
320 IF(PE.GE.STOR+EXCESS+PP(I)) GO TO 230
321 ACTE=PE
322 GO TO 240
323 230 ACTE=STOR+EXCESS+(AMIN1(PP(I),STRMAX))
324 240 STOR =AMIN1(STRMAX,STOR+ACTE+PP(I))
325 SOILM=SOILM+ACTE
326 CONTINUE
327 RETURN
328 END
329 C
330 SUBROUTINE AVC3(DBH,NTREES)
331 COMMON /AVER/ATR(5),ABR(5),YTR,TBR,IAYER
332 COMMON /RUNNR/NVR,KVR,KPNT,KAGE,KTIMES,KFIRST,KLAST
333 COMMON /SIRSP/NSPP
334 DIMENSION DBH(500),NTREES(5)
335 NTREES=0.0
336 BAR=0.0
337 BIT=0.0
338 Y=FLOAT(KVR-1)
339 Z=FLOAT(KVR)
340 N=1
341 DO 10 I=1,NSPP
342 I=I+1
343 IF(NTREES(I).EQ.0) GO TO 10
344 NN=N+NTREES(I)-1
345 STREES=STREES+FLOAT(NTREES(I))
346 BIT=NTREES(I)
347 BIS=0.0
348 DO 9 JJ=N,NN
349 J=JJ
350 BIS=BIS+0.7884*DBH(J)**2
351 BAR=BAR+BIS
352 11 ATR(I)=ATR(I)+BIT
353 ABR(I)=ABR(I)+BIS
354 10 N=N+NTREES(I)
355 YTR=YTR+STREES
356 TBR=TBR+BAR
357 RETURN
358 END
359 C
360 SUBROUTINE QUARYS(DBH,NTREES)

```

JAB03170
JAB03180
JAB03190
JAB03200
JAB03210
JAB03220
JAB03230
JAB03240
JAB03250
JAB03260
JAB03270
JAB03280
JAB03290
JAB03300
JAB03310
JAB03320
JAB03330
JAB03340
JAB03350
JAB03360
JAB03370
JAB03380
JAB03390
JAB03400
JAB03410
JAB03420
JAB03430
JAB03440
JAB03450
JAB03460
JAB03470
JAB03480
JAB03490
JAB03500
JAB03510
JAB03520
JAB03530
JAB03540
JAB03550
JAB03560
JAB03570
JAB03580
JAB03590
JAB03600
JAB03610
JAB03620
JAB03630
JAB03640
JAB03650
JAB03660
JAB03670
JAB03680
JAB03690
JAB03700
JAB03710
JAB03720
JAB03730
JAB03740

```

361 57  FORMAT(' JASOR - A SORCAL FOREST GROWTH SIMULATOR')
362  * (VERSION 2.1)
363  WRITE(6,97)
364  DATA KYES/INY/
365  WRITE(6,1)
366  1  FORMAT(' DO YOU WANT A LIST OF SPECIES NAMES? REPLY Y OR N')
367  READ(6,2) KTEST
368  IF (KTEST .NE. KYES) GO TO 99
369  2  FORMAT(1)
370  WRITE(6,4)
371  4  FORMAT(' THE SPECIES USED ARE: /'
372  * 1 TREMBLING ASPEN(AW)  POPULUS TREMULOIDES /' 2 WHITE SPRUCE(
373  * SW)  PICEA GLAUCA /'
374  99  WRITE(6,5)
375  5  FORMAT(' THERE ARE A NUMBER OF PARAMETERS WHICH MAY BE ALTERED BEFJABO3980
376  * ONE AND DURING /' EXECUTION  RESPOND "Y" TO THE INTERACTIVE QUESTIJABO3980
377  * ONE AND THE PARAMETERS /' THAT MAY BE ALTERED WILL BE DISPLAYED. JABO4000
378  * /' DEFINITIONS OF THE PARAMETERS ARE CONTAINED IN APPENDIX II OF TJABO4010
379  * WE WRITE-UP. /' /'
380  RETURN
381  END
382  C
383  SUBROUTINE INIT2(DSH,NTREES,DSWK,NTREEK,JJ)
384  DIMENSION DSH(1),NTREES(1),DSWK(1),NTREEK(1)
385  COMMON /KILD/ NSGRS(500),DSH(500),KDEAD(5),AREA,KD
386  COMMON /TRACE/ ICES(500),IDSE(500)
387  DO 10 J=1,500
388  DSH(J)=0.0
389  ICE(J)=0
390  CONTINUE
391  DO 11 J=1,500
392  NSGRS(J)=0
393  11  ICES(J)=0
394  DO 12 J=1,5
395  KDEAD(J)=0
396  12  IF (JJ .GT. 1) GO TO 1
397  DO 2 J=1,5
398  NTREEK(J)=NTREES(J)
399  DO 3 K=1,500
400  DSWK(K)=DSWK(K)
401  RETURN
402  1  CONTINUE
403  DO 4 J=1,5
404  NTREES(J)=NTREEK(J)
405  DO 5 K=1,500
406  DSH(K)=DSWK(K)
407  RETURN
408  END
409  C
410  SUBROUTINE GROW(DSH,NTREES)
411  DIMENSION DSH(500),NTREES(5)
412  COMMON /TDATA/G(5),ITYPE(5),AGEXH(5),C(5),F(5)
413  COMMON /KILD/ NSGRS(500),DSH(500),KDEAD(5),AREA,KD
414  COMMON /WDATA/G2(5),G3(5),PHI,SOILO,DEGD,5
415  COMMON /CLIMAT/DMIN(5),DMAX(5),BASET(12),BASEP(12),BASEH
416  COMMON /SPEC/ALNC(5),SINC
417  COMMON /PHOTO/A1,A2,A3
418  NST=0
419  SINC=0.001
420  DO 1 I=1,5

```

```

421  NYBY=NYBY+NTREES(I)
422  IF (NST.EQ.0) RETURN
423  DO 2 I=1,500
424  2  NSGRS(I)=0
425  N=1
426  M=1
427  DO 10 I=1,5
428  IF (NTREES(I).EQ.0) GO TO 10
429  NM=N+NTREES(I)-1
430  DO 3 K=N,M,NM
431  J=KK
432  SLA=0.0
433  SAR=0.0
434  N2=1
435  DO 4 LL=1,5
436  L=LL
437  IF (NTREES(L).EQ.0) GO TO 4
438  N2=N2+NTREES(L)-1
439  DO 7 NM=N2,N3
440  K=NM
441  SAR=SAR+0.7854*DSH(K)**2
442  IF (G2(L)*DSH(K)-G2(L)*DSH(K)**2 .GT. G2(I)*DSH(J)-G3(I)*DSH(J)**2
443  * ISLA=SLA+C(L)*DSH(K)**P(L)/5
444  7  CONTINUE
445  N2=N2+NTREES(L)
446  AL=PHI*EXP(-SLA)
447  CC=(127.+0.25*G2(I)**2/G3(I))*(0.5*G2(I)/G3(I))
448  DINC=G(I)*(DSH(J)**(P(I)-1))*1.0-(127.0*DSH(J)+G2(I)*DSH
449  *(J)**2-G3(I)*DSH(J)**3)/CC/(274.+3.0*G2(I)*DSH(J)
450  * -4.0*G3(I)*DSH(J)**2)*(1.0-SAR/SOILO)*0.0*(DEGD-DMIN(I))*(DMAX(I)
451  * -DEGD)/(DMAX(I)-DMIN(I))**2
452  IF (ITYPE(I).EQ.1) DINC=2.25*(1.0-EXP(-1.135*(AL-0.05)))*DINC
453  IF (ITYPE(I).EQ.2) DINC=(1.0-EXP(-4.54*(AL-0.05)))*DINC
454  IF (ITYPE(I).EQ.3) DINC=AL*(1.0-EXP(A3*(AL-A3)))*DINC
455  IF (DINC.LT.0) DINC=0.0
456  IF (DINC.GT.5.) WRITE(6,5) J,I,DSH(J),DINC
457  5  FORMAT(' DINC IS .GT. 5.0 FOR TREE',I5,' SPECIES',I3,' DSH',F5.
458  *1,' DINC',F8.3)
459  IF (DINC.GT.5) GO TO 91
460  NSGRS(M)=J
461  M=M+1
462  DSH(J)=DSH(J)+DINC
463  9  CONTINUE
464  10  N=N+NTREES(I)
465  RETURN
466  END
467  C
468  SUBROUTINE HLOAD(DSH,NTREES)
469  DIMENSION DSH(500),NTREES(5)
470  RETURN
471  C
472  C
473  SUBROUTINE KILL2(DSH,NTREES,IX)
474  DIMENSION DSH(500),NTREES(5)
475  COMMON /TDATA/G(5),ITYPE(5),AGEXH(5),C(5),F(5)
476  COMMON /KILD/ NSGRS(500),DSH(500),KDEAD(5),AREA,KD
477  COMMON /TRACE/ ICES(500),IDSE(500)
478  COMMON /RUNNR/ NYR, NYR, KPHY, KAGE, KTIMES, KFIRST, KLAST
479  IS = 0
480  N = 0

```

```

481      NE=0
482      DO 100 J=1,5
483      NS=NS+KDEAD(J)
484      IF(J.EQ.3.OR.J.EQ.4.OR.J.EQ.5)GO TO 100
485      IF(NTREES(J).EQ.0)GO TO 100
486      NA = N + 1
487      NN = NTREES(J) + N
488      DO 80 I=NA,NN
489      I=I1
490      CALL RANDOM(IX,R1)
491      IF(DBH(I).LE.34.0.AND.J.EQ.1)PR=4.25
492      IF(DBH(I).LE.34.0.AND.J.EQ.2)PR=3.75
493      IF(DBH(I).GT.34.0.AND.DBH(I).LE.38.0)PR=4.3
494      IF(DBH(I).GT.38.0.AND.DBH(I).LE.38.0)PR=4.8
495      IF(DBH(I).GT.38.0.AND.DBH(I).LE.40.0)PR=5.3
496      IF(DBH(I).GT.40.0.AND.DBH(I).LE.42.0)PR=5.0
497      IF(DBH(I).GT.42.0.AND.DBH(I).LE.44.0)PR=7.5
498      IF(DBH(I).GT.44.0.AND.DBH(I).LE.48.0)PR=9.0
499      IF(DBH(I).GT.48.0.AND.DBH(I).LE.48.0)PR=10.5
500      IF(DBH(I).GT.48.0.AND.DBH(I).LE.50.0)PR=12.0
501      IF(DBH(I).GT.50.0)PR=13.5
502      IF(R1.LT.(PR/ACEMX(J)))GO TO 50
503      73 IF(NGRO(I).EQ.1)GO TO 40
504      GO TO 80
505      ID=ID + 1
506      CALL RANDOM(IX,R2)
507      IF(R2.GT.0.35)GO TO 80
508      IF(KAGE.LT.0)GO TO 70
509      KDEAD(J)=KDEAD(J)+1
510      NS=NS+1
511      NUP=KD-NS
512      IF(NUP.EQ.0)GO TO 55
513      DO 55 KK=1,NUP
514      K=KK
515      IJ=KD-K+1
516      IF(IJ.GT.500)GO TO 55
517      DBH(IJ)=DBH(IJ-1)
518      IDGE(IJ)=IDGE(IJ-1)
519      CONTINUE
520      55 DBH(NS)=DBH(I)
521      IDGE(NS)=IDGE(I)
522      KD=KD+1
523      GO TO 70
524      58 WRITE(6,58)
525      58 FORMAT(' DEAD TREES VECTOR FILLED, RERUN WITH SMALLER PERIOD BETWEEN PRINTOUTS (KPNT)')
526      KPNT=1
527      NTREES(J)=NTREES(J)-1
528      DBH(I) = -1.0
529      CONTINUE
530      80 N = NN
531      CONTINUE
532      DO 200 I=1,500
533      I=I1
534      IF(DBH(I).EQ.0.0)RETURN
535      IF(DBH(I).GT.0.0)GO TO 200
536      DO 120 KK = 1,499
537      K=KK
538      DBH(K) = DBH(K+1)
539      IDGE(K)=IDGE(K+1)
540

```

JAB05130

JAB05140

JAB05300

JAB05310

JAB05320

JAB05330

JAB05340

JAB05350

JAB05360

JAB05370

JAB05380

JAB05390

JAB05400

JAB05410

JAB05420

JAB05430

JAB05440

JAB05450

JAB05460

JAB05470

JAB05480

JAB05490

JAB05500

JAB05510

JAB05520

JAB05530

JAB05540

JAB05550

JAB05560

JAB05570

JAB05580

JAB05590

JAB05600

```

541      120 CONTINUE
542      DBH(500) = 0.0
543      IF(DBH(1).LT.0.0)GO TO 110
544      200 CONTINUE
545      RETURN
546      END
547      C
548
549      SUBROUTINE OUTPY(DBH,NTREES)
550      DIMENSION DBH(500),BDN(500),NTREES(5),IDM(500),BAR(5)
551      COMMON/TOPTA/C(5),ITYPE(5),ACEMX(5),C(5),P(5)
552      COMMON/KILD/NGRO(500),DDBH(500),KDEAD(5),AREA,KD
553      COMMON/TRACE/IGES(500),IDGE(500)
554      COMMON/RUNNR/NYR,KYR,KPNT,KAGE,KTIME,KFIRST,KLAST
555      COMMON/KILLR/LOG,ALIMIT(5)
556      COMMON /PLOTO/ IELEV,IROCK,TILL,SOILM,TEXT,EXCESS
557      COMMON/MDATA/S2(5),S3(5),PHI,SOILO,DEGD,0
558      COMMON/CLIMAT/DWIN(5),DWA(5),BASET(12),BASEP(12),BASEH
559      COMMON /BIRTHK/ASPPWT,WMIN(5),WMAX(5)
560      COMMON/SIRSP/NSPP
561      COMMON/AVER/ATR(5),ABR(5),YTR,YBR,IAYER
562      COMMON/OUTCON/NOBDM
563      IF(NODB.NE.0)GO TO 15
564      WRITE(6,11)
565      11 FORMAT('/// YEAR SPEC. NUM. BASAR. ',20X,'DBH')
566      15 WRITE(6,21) KYR
567      21 FORMAT('S')
568      25 NDEAD=0
569      NTOT=0
570      DO 1 I=1,5
571      NDEAD=NDEAD+KDEAD(I)
572      NTOT=NTOT + NTREES(I)
573      IF(NTOT.EQ.0)GO TO 100
574      N=1
575      AREA=0.0
576      WLEAF=0.0
577      SIGMA=0.0
578      SPWT=0.0
579      AWWT=0.0
580      TEAR=0.0
581      DO 20 I=1,5
582      I=I1
583      BAR(I)=0.0
584      IF(NTREES(I).EQ.0)GO TO 30
585      NN=N+NTREES(I) - 1
586      NI=NTREES(I)
587      DO 50 JJ=N,NN
588      J=JJ
589      TREE=0.0
590      WT=0.0
591      FOL=0.0
592      IF(I.EQ.1)GO TO 23
593      IF(DBH(J).GE.4.021)GO TO 25
594      WT=((10.0**0.15))*((DBH(J)/2.54)**2.48)/2.2
595      SPWT=SPWT+WT
596      FOL=(C(I)*DBH(J)**F(I))/1000.0
597      GO TO 28
598      25 TREE=7.89727-(3.23888*DBH(J))+0.43412*DBH(J)**2+(0.000
599      *S=DBH(J)**3)
600      FOL=(C(I)*DBH(J)**F(I))/1000.0

```

JAB05610

JAB05620

JAB05630

JAB05640

JAB05650

JAB05660

JAB05670

JAB05680

JAB05690

JAB05690

JAB05690

JAB05690

JAB05690

JAB05690

JAB05690

JAB05690

JAB05690

JAB05690

JAB05690

JAB05690

JAB05690

JAB05690

JAB05690

JAB05690

JAB05690

JAB05690

JAB05690

JAB05690

JAB05690

JAB05690

JAB05690

JAB05690

JAB05690

JAB05690

JAB05690

JAB05690

JAB05690

JAB05690

JAB05690

JAB05690

JAB05690

JAB05690

JAB05690

JAB05690

JAB05690

JAB05690

JAB05690

JAB05690

JAB05690

JAB05690

JAB05690

```

001      AYT(I)=0
002      ABR(I)=0.0
003      45 CONTINUE
004      TTR=0.0
005      TBR=0.0
006      GO TO 200
007      100 WRITE(6,3) KVR
008      3 FORMAT(10X,'YEAR',IS,' NO TREES LIVING')
009      THEEND=1000.0
010      DO 298 I=1,5
011      THEEND=AMIN1(THEEND,DMIN(I))
012      IF (DEGD .GT. THEEND) GO TO 298
013      WRITE(6,297)
014      297 FORMAT(10X,'NONE OF THE SPECIES YOU ARE USING CAN EXIST WITH THIS
015      * CLIMATE')
016      STOP
017      298 THEEND=1000.0
018      DO 298 I=1,5
019      298 THEEND=AMIN1(THEEND,WMIN(I))
020      IF (SOILM .GT. THEEND) GO TO 200
021      WRITE (6,293)
022      293 FORMAT(10X,'THE SPECIES YOU HAVE SELECTED ARE INCOMPATIBLE WITH
023      * THE CLIMATE')
024      STOP
025      200 IF(LOS .LT. 0)GO TO 60
026      CALL CUT2(DBH,NTREES)
027      GO TO 95
028      50 CONTINUE
029      KDI=1
030      IF(NDEAD .EQ.0) RETURN
031      WRITE (6,201)
032      201 FORMAT(' DEAD TREES SINCE LAST PRINTOUT')
033      N=1
034      DO 95 I=1,5
035      I=I
036      IF(KDEAD(I) .EQ.0) GO TO 95
037      NN=N+KDEAD(I) - 1
038      N1=KDEAD(I)
039      DO 95 J=1,N1
040      N2=J+N-1
041      DBH(J)=DBDH(N2)
042      IDH(J)=IDGE(N2)
043      95 CONTINUE
044      N2=MIN0(7,N1)
045      WRITE(6,4) 1,KDEAD(I),(DBH(J),IDH(J),J=1,N2)
046      IF(N1 .GT.7) WRITE(6,6) (DBH(J),IDH(J),J=8,N1)
047      6 FORMAT(27X,P9.3,14,P9.3,14,P9.3,14,P9.3,14,P9.3,14,P9.3,14,P9.
048      *3,14)
049      4 FORMAT(5X,15,17,10X,V(P9.3,14))
050      N=N+KDEAD(I)
051      95 CONTINUE
052      DO 299 I=1,5
053      KDEAD(I)=0
054      299 CONTINUE
055      300 RETURN
056      END
057      C
058      -----
059
060      BLOCK DATA
061      COMMON/DTDATA/2(S),ITYPE(S),AERWX(S),C(S),P(S)

```



```

721 COMMON/COMMON/RVR, I, KPNT, KAGE, KTIMES, KPTSTY, KLAST
722 COMMON/TRACE/IGES(500), IDGE(500)
723 COMMON/WDATA/92(5), 93(5), PHI, SOILQ, DECD, S
724 COMMON/CLIMAT/DMIN(5), DMAX(5), BASEP(12), BASEN
725 COMMON /PLOTG/ IELEV, IRDCK, TILL, SOILM, TEXT, EXCESS
726 COMMON /BIRTHK/ASPWT, UMIN(5), WMAX(5)
727 COMMON/KILLR/LQG, ALIMIT(5)
728 COMMON/AVR/ATR(5), ABR(5), TTR, TBR, IAYER
729 COMMON/BIRSP/NSPP
730 COMMON/SAPLG/SAPNU(5)
731 COMMON/PHOTO/A1, A2, A3
732 COMMON/SPEC/AINC(5), SINC
733 DATA ATR, ABR, TTR, TBR, IAYER/S=0.0, S=0.0, 0.0, 0.0, 0.0/
734 DATA KTIMES/1/, KFIRST/0/, KLAST/208/, RVR/500/, KPNT/5/, KAGE/-1
735 * / LQG/-1/
736 DATA E/190.0, 122.5, 121.0, 155.5, 108.0/
737 DATA C/5.0, 13.0, 0.0, 0.0, 0.0/
738 DATA F/1.9000, 2.0000, 0.0, 0.0, 0.0/
739 DATA AGEMX/120., 250., 200., 200., 245./
740 DATA ITYPE/1, 3, 3, 1, 1/
741 DATA S2/76.5, 70.4, 80.3, 83.4, 81.7/
742 DATA S3/532., 385., 348., 290., 722/
743 DATA EXCESS/0.25/, PHI/1.0/, SOILQ/2.0E4/, DECD/3000.0/, D/S.5E4/
744 DATA DMIN/950.0, 750.0, 9999.9, 9999.9, 9999.9/
745 DATA DMAX/5200.0, 3500.0, 0.0001., 0.0001., 0.0001/
746 DATA BASEP/2.1, 13.5, 21.4, 36.9, 48.5, 54.9, 59.2, 57., 48.0, 28.1, 20.
747 * 7.3, 4/
748 DATA BASEN/1.15, 0.95, 0.95, 1.05, 2.13, 3.51, 4.0, 3.48, 1.38, 1.05, 0.
749 * 93.1, 05/
750 DATA ASPWT/550.0/, BASEN/2431.1/
751 DATA TEXT/150.0/, IELEV/741/, IRDCK/0/, TILL/10.0/
752 DATA WMIN/150.0, 150.0, 9999.9, 9999.9, 9999.9/
753 DATA WMAX/500.0, 500.0, 0.0001., 0.0001., 0.0001/
754 DATA AINC/.10., .05., .05., .10., .07/
755 DATA NSPP/5/
756 DATA A1/1.0/, A2/-4.84/, A3/0.05/
757 DATA SAPNU/2.0, 2.0, 0.0, 0.0, 0.0/
758 END
759 -----
760 SUBROUTINE RANDOM (IX, R)
761 C
762 C PATCH TO CALL RANF AGS 22 MAY 78
763 R=RANF(IX)
764 RETURN
765 END

```

End of file

Sample Run of JABOR

* SIG DEST 8

* DEST 17:12:00, Apr 12/85; last 17:10:17

* JAB: C+CSL18

* 17:12:18

JABOR - A BOREAL FOREST GROWTH SIMULATOR

DO YOU WANT A LIST OF SPECIES NAMES? REPLY Y OR N

Y

THE SPECIES USED ARE:

1. TREMBLING ASPEN(AW) POPULUS TREMULOIDES
2. WHITE SPRUCE(SW) PICEA GLAUC

THERE ARE A NUMBER OF PARAMETERS WHICH MAY BE ALTERED BEFORE AND DURING EXECUTION. RESPOND "Y" TO THE INTERACTIVE QUESTIONS, AND THE PARAMETERS THAT MAY BE ALTERED WILL BE DISPLAYED.
DEFINITIONS OF THE PARAMETERS ARE CONTAINED IN APPENDIX II OF THE WRITE-UP.

I/O CHANGES? Y OR N?

Y

ENTER ANIO CHANGES=KFIRST,KLAST,KTIME,KPNT,KAGE,NYR,NDOBH,IAVER

ANIO NYR=30 SEND

PLOT CHANGES? Y OR N?

Y

ENTER ANPT CHANGES IN IELEV, IROCK, IX, TILL, TEXT, DMIN, DMAX, WMIN, WMAX
ASPTW, ALIMIT, LOC, NTREES, DBH: PHI, SOILO, ITYPE, AGEMX, B2, B3, NSPP,
SAPNU, AINC, A1, A2, A3, C, D, F, G

ANPT IX=12345678 SEND

***** IX = 12345678

PLOT NUMBER	ELEVATION (METERS)	SOIL DEPTH	PERCENT ROCK	GROWING DEGREE DAYS	INDEX OF ACTUAL ET
0	741	10.0	0	1807.8	384.4

YEAR	SPEC.	NUM.	SASAR.	DBH
0				
YEAR 0 NO TREES LIVING				
5				
1	25	34.230	1.188 1.777 2.249 2.188 1.088 2.039 1.883 1.418 2.143 0.822	1.088
2	3	3.411	1.277 1.308 0.584 1.271 0.789 0.868 0.309 1.114 1.208 0.774	1.088
28		37.842	LEAF AREA = 0.008	
BIOMASS: AW: 8.408 SW: 0.321 TOT: 5.730				
CHANGES? Y OR N?				

YEAR	SPEC.	NUM.	SASAR.	DBH
10				
1	38	172.088	2.742 2.487 4.043 3.848 2.878 3.787 3.590 3.042 3.917 2.888	2.888
			2.888 1.787 2.849 2.178 1.883 2.827 2.138 2.888 2.194 1.332	2.888
			1.819 1.407 2.418 1.488 2.143 1.078 2.033 1.307 1.317 1.820	1.217
			1.488 1.702 1.882 0.829 0.728 1.278 0.501	

YEAR	SPEC.	NUM.	SASAR.	DBH
15				
1	33	434.833	4.888 8.977 8.878 8.713 8.490 4.887 8.838 4.881 4.737 3.483	2.888
			4.882 3.824 3.872 4.444 3.878 4.388 3.841 2.883 4.488 3.285	2.888
			4.183 3.088 2.849 3.782 2.888 2.871 2.287 2.739 3.047 3.385	3.342
2	7	48.082	1.887 4.818 3.488 3.473 2.348 2.189 2.114 0.884	
40		483.898	LEAF AREA = 0.071	
BIOMASS: AW: 38.771 SW: 8.710 TOT: 43.481				
CHANGES? Y OR N?				
20				
1	28	780.701	8.478 7.980 7.873 7.441 8.824 7.788 8.884 8.283 8.884 8.788	4.277
			8.814 8.337 8.732 8.243 8.788 4.881 8.388 8.088 8.084 4.888	4.277
			8.888 4.818 4.832 8.089 4.823 8.188 8.148 3.480	
2	8	113.830	8.843 8.182 8.178 3.784 3.888 3.808 1.819 1.814	
37		904.331	LEAF AREA = 0.138	
BIOMASS: AW: 108.078 SW: 17.488 TOT: 125.538				
CHANGES? Y OR N?				
25				
1	24	1084.188	8.403 8.818 8.380 8.781 8.881 7.184 8.818 7.888 7.380 7.808	8.808
			8.142 7.878 8.474 8.800 7.848 8.888 8.088 7.488 8.421 8.438	8.808
			8.887 8.227 0.873 8.888 8.182 8.881 8.488 8.378 8.278 3.330	2.818
2	8	217.100	8.838 7.000 8.881 8.488 8.378 8.278 3.330 2.818 0.488	
33		1271.288	LEAF AREA = 0.201	
BIOMASS: AW: 181.893 SW: 38.202 TOT: 221.098				
CHANGES? Y OR N?				
28				
1	23	1078.874	8.788 8.780 10.143 8.887 7.828 8.881 8.088 7.784 7.883 8.823	7.388
			8.081 8.838 7.370 8.334 7.033 8.438 7.831 8.782 8.788 7.278	7.388
			8.881 0.740 8.820 7.370 7.380 8.887 8.730 8.837 3.840 3.111	0.882
2	8	243.033		

32 1318.057 LEAF AREA = 0.213
 BIOMASS: AW: 201.570 SW: 45.847 TOT: 247.417
 CHANGES? Y OR N?

YEAR	SPEC	NUM	BASAL	DBH											
27	1	22	1112.084	9.174	10.188	10.830	9.353	7.901	8.423	8.128	8.358	8.903	8.428	8.934	
				7.201	7.840	8.701	7.398	8.785	8.204	7.143	7.158	7.643	7.725		
				0.931											
	2	10	271.578	9.308	7.743	7.722	8.162	8.084	8.980	3.957	3.414	0.738	1.000		

32 1383.870 LEAF AREA = 0.227
 BIOMASS: AW: 219.482 SW: 53.425 TOT: 272.898
 CHANGES? Y OR N?

YEAR	SPEC	NUM	BASAL	DBH											
28	1	23	1214.662	9.557	10.558	10.917	9.736	8.272	8.798	8.488	8.732	8.281	8.798	8.286	
				7.582	8.007	9.075	7.783	7.142	8.578	7.502	7.518	8.009	8.091		
				1.143	0.487										
	2	10	301.385	9.892	8.115	8.095	8.518	8.439	8.334	4.278	3.722	0.888	1.183		

33 1516.047 LEAF AREA = 0.249
 BIOMASS: AW: 254.849 SW: 81.559 TOT: 316.107
 CHANGES? Y OR N?

YEAR	SPEC	NUM	BASAL	DBH											
29	1	23	1321.021	9.938	10.940	11.302	10.117	8.640	9.171	8.884	9.103	9.657	9.189	8.636	
				7.920	8.372	9.646	8.125	7.488	8.942	7.858	7.874	8.372	8.454		
				1.371	0.634										
	2	10	333.009	10.077	8.488	8.487	8.878	8.798	8.689	4.803	4.035	1.057	1.382		

33 1554.030 LEAF AREA = 0.272
 BIOMASS: AW: 293.287 SW: 70.840 TOT: 363.828
 CHANGES? Y OR N?

YEAR	SPEC	NUM	BASAL	DBH											
30	1	23	1431.129	10.317	11.322	11.683	10.495	9.008	9.542	9.234	9.470	10.029	9.537	8.981	
				8.278	8.734	9.615	8.488	7.847	9.307	8.210	8.228	8.732	8.814		
				1.613	0.802										
	2	11	386.448	10.481	8.881	8.839	7.234	7.183	7.048	4.931	4.382	1.243	1.585		
				0.041											

34 1787.574 LEAF AREA = 0.297
 BIOMASS: AW: 335.605 SW: 80.270 TOT: 415.874
 CHANGES? Y OR N?

WANT TO TRY AGAIN?

N
 # 17:14:01 T=0.58 RC=0

PC A
 > ADDITIONAL USER INFORMATION
 >
 > 1. When making interactive alterations, the first space must be left blank,
 > so that the first "A" is typed in the second column.
 >
 > 2. When altering species-specific parameters, enter the species number
 > between parentheses following the parameter to be altered. For example:
 > SNPT S(1)=value,SEND
 >
 > 3. A carriage return with no entry will also serve as a negative response.
 >
 WCONTR *PRINT* PRINTON=ONESIDE PACKAGE=LOOSE
 # *PRINT* assigned receipt number 820189
 # *PRINT* 820189 held
 #C *MSOURCE=QSP *PRINT*

Index Of Parameters That Can Be Changed Interactively

<u>NAME</u>	<u>DESCRIPTION</u>
A1,A2,A3	Variables used in calculation of the R(AL) function for very tolerant trees (ITYPE=3); not used in present version. Defaults A1: 1.0, A2: -4.64, A3: 0.05
AGEMX	Species-specific maximum observed age (yr.). Defaults: Sw (white spruce): 250, Aw (trembling aspen): 125 yr.
AINC	Species-specific minimum diameter increment (cm) which a tree must attain to avoid being subjected to a probability of suppression mortality. Defaults: Sw: 0.08, Aw: 0.10
ALIMIT	Species-specific diameter (cm) of tree to be removed from the plot by logging; can be used only if the parameter LOG is set at or greater than zero.
ASPEN	Total plot leaf weight (gm) below which trembling aspen can be introduced in relatively large numbers. Default=550.0
B2, B3	Species-specific constants in the growth rate equation. Defaults: B2: Sw: 70.4, Aw: 74.5; B3: Sw: 0.385, Aw: 0.532
C	Species-specific leaf area constant (gm/cm ²). Defaults: Sw: 13.0, Aw: 5.0
D	Constant used in calculation of plot shading. Default=95,000.0
DBH	Vector containing DBH (cm) ^a of each tree.
DEGD	User specified plot growing degree-days, which can be substituted for value calculated in SITE2. Default: 3000.0
DMIN	Species-specific minimum growing degree-days required for regeneration and growth. Defaults: Sw: 750.0, Aw: 950.0
DMAX	Species-specific maximum growing degree-days required for regeneration and growth. Defaults: Sw: 3500.0, Aw: 5200.0

F	Species-specific exponent used in calculation of leaf weight; also required in growth rate equation. Defaults: Sw: 2.0, Aw: 1.9
G	Species-specific growth rate constant. Defaults: Sw: 122.5, Aw: 190.0.
IAVER	Controls output of species averages for number of trees and basal area. If IAYER is greater than zero, averages are displayed. Default: 0
IELEV	Elevation of plot (m) Default: 741.0 (elevation of Whitecourt weather station)
IROCK	Per cent rock on the soil surface; used to calculate total volume of soil available for water storage. Default: 0
ITYPE	Species-specific shade tolerance class; 1=intolerant, 2=tolerant. Defaults: Sw: 2, Aw: 1
IX	Starting point for the pseudo-random generator. Default: 987643
KAGE	Determines whether age and diameter of trees at death will be recorded and displayed. If KAGE is greater than or equal to zero, records will be kept and displayed. Default: 0
KFIRST	The number of the first data plot to be read in and used by the program. Not used in present version.
KLAST	The number of the last data plot to be read in and used by the program. Not used in present version.
KPNT	The number of years between print-outs. Default: 1
KTIMES	The number of sequential runs for a plot, using different random number starting points. Default: 1
LOG	The maximum diameter (cm) of tree to be removed from the plot by logging. Default=-1
NODBH	Controls output of DBH's of trees. If NODBH is greater than 0, DBH's are not printed out. Default: 0
NSPP	Number of species used in the simulation runs. Default: 5
NTREES	The number of live trees per species on the plot.

NYR Number of years for the simulation run. Default:
 200

PHI Relative light level above the forest canopy.
 Default: 1.0

SAPNU Maximum number of white spruce saplings that can
 be added to a plot each year; default: 2.0.
 Maximum number of trembling aspen saplings that
 can be randomly added to a plot each year;
 default: 2.0

SOILQ The maximum basal area (cm²) a plot can support.
 Default: 20,000.0

TEXT The water-holding capacity (mm/m) of the soil.
 Default: 250.0

TILL Plot soil depth (m), used to calculate the amount
 of water storage in the soil. Default: 10.0

WMIN Species-specific minimum actual evapotranspiration
 level (mm) required for regeneration and growth.
 Defaults: Sw: 150.0, Aw 150.0

WMAX Species-specific maximum actual evapotranspiration
 level (mm) required for regeneration and growth.
 Defaults: Sw: 600.0, Aw: 600.0

XI. APPENDIX III: LIVING BIOMASS EQUATIONS USED IN JABOR

A. White Spruce

1. Total-tree aboveground, DBH outside bark < 4.021 cm:
 $\text{LOG WT} = 0.150 + (\text{LOG D})$
 where:
 WT=dry weight (lb.)
 D=DBHOB (in.)
 from Baskerville (1965).
2. Total-tree aboveground minus foliage, DBHOB $\geq$ 4.021 cm:
 $\text{WT} = 7.69727 - 3.23895 + 0.43412D^2 + 0.0006D^3$
 where:
 WT=dry weight (kg)
 D=DBHOB (cm)
 from Singh (1982).
3. Foliage (used to derive values for C and F):
 $\ln \text{WT} = -4.3267 + 2.1816(\ln D)$
 where $\ln$ =natural logarithm
 WT=dry weight (kg)
 D=DBHOB (cm)
 from Freedman et al. (1982).

B. Trembling Aspen

1. Total-tree aboveground, DBHOB < 5.028 cm:
 $\text{LOG WT} = -1.1115 + 2.3466(\text{LOG D})$
 where:
 WT=dry weight (lb.)
 D=DBHOB (in.)
 from Peterson et al. (1970).
2. Total-tree aboveground minus foliage, DBHOB $\geq$ 5.028 cm:
 $\text{WT} = 23.61521 - 7.88903D + 0.78372D^2 - 0.00362D^3$
 where:
 WT=dry weight (kg)
 D=DBHOB (cm)
 from Singh (1982).
3. Foliage (used to derive values for C and F):
 $\ln \text{WT} = 4.0359 + 1.6093(\ln D)$
 where:
 $\ln$ =natural logarithm
 WT=dry weight (kg)
 D=DBHOB (cm)
 from Freedman et al. (1982).

XII. APPENDIX IV: TABLES OF RESULTS

1. Table A4.1. Predictions of JABOR of average basal area compared to average basal values of the validation data: white spruce, trembling aspen, total plot.
2. Table A4.2. Predictions of JABOR of average frequency compared to average frequencies of the validation data: white spruce, trembling aspen, total plot.
3. Table A4.3. Biomass predictions of JABOR: white spruce, trembling aspen, total plot.

Table A4.1. Predictions of JABOR of average basal area compared to average basal area values of the validation data: white spruce, trembling aspen, total plot.

YEAR	BASAL AREA (cm / 0.01 ha)					
	WHITE SPRUCE		TREMBLING ASPEN		MIXEDWOOD STAND	
	P	O	P	O	P	O
30	160	727	1218	1739	1379	2464
35	242	337	1495	1600	1754	1935
40	347	769	1719	1845	2105	2313
45	509	711	1632	3109	2331	3820
50	673	---	1653	---	2535	---
55	813	731	1879	2457	2792	3193
60	1020	377	2071	2634	3091	2911
65	1211	1419	2075	1995	3255	2455
70	1367	1474	1955	1822	3343	3255
75	1624	2301	1925	1933	3549	3324
80	1800	2226	1922	1851	3422	3007
85	2182	3075	1859	1240	4021	4315
90	2294	2842	1784	1072	4079	4014
95	2429	1915	1882	1952	4111	3870
100	2651	2188	1821	2021	4182	4185
105	2721	2805	1927	1823	4255	4729
110	2980	2422	1274	1042	4254	4455
115	3265	2435	1325	2113	4592	4544
120	3242	3403	1294	534	4518	3937
125	2517	2041	1114	1551	4621	3592
130	3525	2870	824	553	4480	3553
135	3483	2472	839	602	4323	4074
140	3500	3214	729	300	4235	3514
145	3345	---	719	---	4055	---
150	3115	3277	457	255	3902	3555
155	3091	---	355	---	3449	---
160	3105	522	242	35	3244	557
165	3050	2539	185	740	3215	3275
170	3051	---	100	---	3181	---
175	2527	2575	119	4	2955	3575
180	2711	---	124	---	2645	---
185	2749	---	111	---	2550	---
190	2555	---	55	---	2544	---
195	2529	---	52	---	2721	---
200	2421	---	27	---	2445	---
210	2052	---	24	---	2075	---
220	2127	---	50	---	2177	---
230	2355	---	55	---	2425	---
240	2730	---	54	---	2514	---
250	2772	---	55	---	2527	---
260	3113	---	45	---	2151	---
270	2303	---	50	---	2253	---
280	2551	---	35	---	2555	---
290	3029	---	50	---	3075	---

300	3331	---	35	---	3355	---
310	2911	---	52	---	2553	---
320	2554	---	44	---	2515	---
330	2550	---	15	---	2559	---
340	2775	---	40	---	2515	---
350	2515	---	45	---	2555	---
360	1854	---	22	---	1575	---
370	1851	---	45	---	2005	---
380	3333	---	55	---	2402	---
390	3252	---	107	---	2355	---
400	2753	---	50	---	2573	---
410	3050	---	112	---	3192	---
420	2555	---	74	---	2550	---
430	3455	---	25	---	3450	---
440	3291	---	19	---	3210	---
450	3154	---	25	---	3150	---
460	2903	---	15	---	2515	---
470	2777	---	27	---	2504	---
480	2504	---	35	---	2540	---
490	2757	---	24	---	2751	---
500	2555	---	15	---	2552	---

P: predicted
O: observed

Table A4.2. Predictions of JABOR of average frequency compared to average frequencies of the validation data: white spruce, trembling aspen, total plot.

YEAR	FREQUENCY (no./0.01 ha)					
	WHITE SPRUCE		TREMBLING ASPEN		MIXEDWOOD STAND	
	P	O	P	O	P	O
30	7.40	8.90	18.80	18.83	27.20	21.53
35	8.70	8.40	17.00	11.80	28.70	17.30
40	8.30	8.70	18.70	11.27	28.00	18.87
45	8.90	8.60	13.30	22.40	23.20	32.00
50	8.70	---	11.50	---	21.20	---
55	8.90	3.87	10.20	11.78	20.10	18.53
60	10.00	2.85	9.30	10.48	19.30	13.30
65	8.50	7.34	7.90	3.10	17.40	10.44
70	8.80	8.49	8.44	4.80	18.24	10.88
75	8.90	12.21	8.80	2.74	18.70	14.88
80	8.98	8.18	8.12	3.05	18.10	9.20
85	10.20	11.48	4.00	3.22	18.10	14.70
90	8.50	11.30	3.94	2.30	12.44	13.80
95	8.40	8.51	2.84	2.55	12.34	9.08
100	8.40	7.32	3.04	2.38	12.44	10.70
105	8.30	7.84	2.20	2.53	11.50	10.47
110	8.50	8.89	2.24	1.47	11.74	11.38
115	8.50	8.05	1.94	3.08	11.44	9.13
120	8.80	8.28	1.72	0.78	11.22	7.13
125	9.20	4.28	1.72	1.42	10.82	3.88
130	9.20	3.48	1.32	0.48	10.82	3.88
135	8.50	8.53	1.08	0.83	9.88	8.18
140	8.84	7.43	1.02	0.81	9.78	8.04
145	8.48	---	0.80	---	9.28	---
150	8.78	8.54	0.82	0.88	9.40	10.42
155	8.38	---	0.38	---	8.74	---
160	7.80	2.10	0.30	0.21	8.10	2.31
165	8.34	8.81	0.20	1.28	8.84	8.08
170	7.92	---	0.32	---	8.24	---
175	8.12	11.40	0.40	0.22	8.52	11.82
180	8.04	---	0.80	---	8.84	---
185	7.50	---	0.72	---	8.22	---
190	7.40	---	0.78	---	8.18	---
195	8.10	---	0.82	---	8.72	---
200	8.10	---	0.78	---	8.88	---
210	8.40	---	1.10	---	8.80	---
220	9.00	---	1.80	---	10.80	---
230	9.40	---	1.80	---	11.00	---
240	9.30	---	1.10	---	10.40	---
250	8.80	---	0.80	---	10.30	---

P: predicted
O: observed

250	8.70	---	0.80	---	8.80	---
270	8.00	---	1.00	---	9.00	---
280	8.30	---	0.80	---	9.10	---
290	9.10	---	0.70	---	9.80	---
300	9.10	---	0.70	---	9.80	---
310	8.90	---	0.70	---	9.80	---
320	10.00	---	0.80	---	10.50	---
330	9.40	---	0.50	---	9.90	---
340	9.10	---	0.80	---	9.90	---
350	8.80	---	0.70	---	9.20	---
360	8.10	---	1.00	---	9.10	---
370	8.80	---	1.80	---	10.40	---
380	8.90	---	1.40	---	10.30	---
390	8.80	---	1.30	---	10.10	---
400	8.50	---	1.10	---	9.80	---
410	10.00	---	1.20	---	11.20	---
420	9.20	---	0.90	---	10.10	---
430	10.30	---	0.70	---	11.00	---
440	9.90	---	0.70	---	10.20	---
450	8.30	---	0.80	---	9.30	---
460	8.50	---	0.80	---	9.20	---
470	8.80	---	0.80	---	9.40	---
480	8.70	---	0.80	---	9.50	---
490	8.90	---	0.80	---	9.40	---
500	8.40	---	0.80	---	10.00	---

Table A4.3. Biomass predictions of JABOR: white spruce, trembling aspen, total plot.

YEAR	BIOMASS (kg/0.01 ha)		
	WHITE SPRUCE	TREMBLING ASPEN	MIXEDWOOD STAND
30	38	294	328
35	55	450	515
40	103	801	709
45	159	715	877
50	225	799	1025
55	285	854	1139
60	355	885	1231
65	453	1004	1462
70	552	889	1542
75	550	1002	1552
80	777	1030	1807
85	917	1012	1928
90	955	1010	1995
95	1055	945	2014
100	1127	903	2030
105	1227	895	2123
110	1384	798	2182
115	1475	780	2255
120	1543	772	2315
125	1538	870	2308
130	1559	811	2172
135	1567	480	2147
140	1568	428	2095
145	1532	350	1991
150	1527	274	1801
155	1498	205	1700
160	1468	137	1595
165	1431	107	1549
170	1447	81	1525
175	1337	70	1407
180	1182	75	1237
185	1241	81	1302
190	1227	47	1274
195	1257	50	1307
200	1155	11	1165
210	841	5	845
220	873	15	888
230	1058	15	1058
240	1255	32	1255
250	1295	30	1325
260	925	15	944
270	953	17	960
280	1194	5	1200

290	1354	5	1403
300	1555	11	1578
310	1355	19	1385
320	1177	15	1195
330	1244	5	1249
340	1305	3	1313
350	1171	15	1189
360	785	5	771
370	570	14	584
380	1051	23	1074
390	1022	32	1054
400	1277	29	1308
410	1424	40	1484
420	1390	25	1415
430	1537	7	1544
440	1552	8	1558
450	1500	12	1512
460	1355	3	1358
470	1300	5	1308
480	1200	13	1213
490	1275	22	1297
500	1225	12	1241

P: predicted
O: observed

XIII. APPENDIX 5: CASE STUDY DATA

1. Table A5.1. Case study III: mean annual increment of average basal area of white spruce per age of removal of trembling aspen

Table AS.1. Case Study III: mean annual increment of average basal area of white spruce per age of removal of trembling aspen.

	MEAN ANNUAL INCREMENT (cm/yr)											
	CONTR	Age of Treatment (yr)										
		0	30	40	50	60	70	80	90	100	110	
S T A N D A R D E Y R	30	5.51	5.75	4.78	4.73	5.00	5.25	5.53	4.84	5.52	7.02	5.54
	40	9.74	8.84	5.51	7.73	8.53	7.98	9.41	8.04	8.50	10.32	9.51
	50	13.70	13.72	12.88	12.08	11.98	11.15	12.58	10.81	12.57	11.30	13.31
	60	17.31	18.48	17.48	15.50	15.91	15.29	15.39	14.41	15.71	13.55	17.81
	70	19.74	23.50	22.21	21.32	21.58	19.51	20.88	18.08	19.05	18.11	20.51
	80	23.48	28.41	25.52	25.55	25.23	24.49	24.82	20.70	20.22	18.15	22.00
	90	25.58	31.35	31.24	29.01	28.17	28.72	25.89	23.91	24.55	21.13	25.30
	100	25.81	34.70	33.25	31.14	30.14	28.89	26.82	27.32	25.86	22.78	28.89
	110	26.52	33.95	32.59	34.12	30.20	31.02	28.92	30.39	29.40	24.50	25.89
	120	28.22	31.78	32.14	32.85	30.02	31.04	28.51	31.41	30.89	24.30	24.14
	130	28.74	30.42	31.49	29.39	29.37	31.14	28.83	32.08	25.49	23.50	23.00
	140	24.27	28.38	28.35	27.55	25.08	28.47	27.73	30.20	24.89	21.65	22.81
	150	30.88	25.75	24.09	25.25	22.11	24.92	21.80	27.31	23.67	20.79	21.32

